

SUCCESSION AND DIVERSITY IN THE PLEISTOCENE CORAL REEFS OF THE KENYA COAST

by J. A. CRAME

ABSTRACT. Many of the faunal changes that occur in vertical sections through the late Pleistocene coral reefs of the Kenya coast can be interpreted within the context of ecological succession. A number of instances of one set of species 'preparing the ground' for the next were found but these are all restricted to the earliest stages of primary successions. Clearly defined vertical zones are rare and much of the succession on established reefs appears to have been rather random and unstructured. However, this is precisely what some modern theories predict.

Some pattern is provided to early succession by a series of competitive replacements that typically result in domination by faster-growing branching and platy-encrusting species, especially acroporids. Longer-term trends are more cryptic, but there is some evidence to suggest that branching assemblages may eventually be replaced by assemblages of large doming-massive corals.

Diversity is largely controlled by localized environmental disturbances which promote the establishment of either mixed or monospecific coral stands. In a few instances diversity increases continually through succession, and it would appear that 'equilibrium' coral assemblages can be built up within a comparatively short period of reef growth.

THERE is much scope for palaeontologists to interpret some of the many vertical sequences at their disposal in terms of ecological succession (e.g. Valentine 1973, p. 324; Gould 1976, p. 225). Previous emphasis in vertical faunal studies has traditionally been from an evolutionary standpoint, but now many sequences are recognized to be more or less complete records of *in situ* ecological successions. Detailed study of fossil successions, in both reef and non-reef environments (e.g. Johnson 1972; Bretsky and Bretsky 1975, 1976; Walker and Alberstadt 1975; Walker and Parker 1976; Alberstadt and Walker 1976), is leading to the accumulation of valuable data on the mechanisms and rates of community change, much of which can be directly used to test some of the many hypotheses and models of theoretical ecology.

This work concentrates on the study of ecological succession in reef environments and in particular describes the faunal changes revealed in a series of vertical sections through the late Pleistocene coral reefs of the Kenya coast. As a prelude, a brief review is given of previous studies of reef succession and an attempt is made to establish the theoretical framework on which these have been based. Such has been the growth in both theoretical ecology and palaeoecology in recent years that many established theories have been critically reappraised and plausible alternatives suggested. Nowhere is this more so than in the field of community dynamics.

FOSSIL REEF SUCCESSION

Previous studies of fossil reef succession have been profoundly influenced by the seminal work of Lowenstam (1950, 1957) on the Silurian reefs of the Great Lakes area. Based on the physical factors of water depth and wave resistance, Lowenstam delineated three stages in the sequential development of reefs. A reef was established during a quiet-water stage, given substance during the semi-rough-water stage, and finally consolidated into a complex community of interdependent organisms during the rough-water or wave-resistant stage. Nicol (1962) later interpreted these stages

as the pioneer, pre-climax, and climax stages of an ecological sere. This model of reef development proved intrinsically satisfying to geologists, for many reefs showed a demonstrable increase in complexity through time. New groups of both reef-builders and dwellers were continually incorporated into the framework, and these in turn provided a continual supply of novel biospace for further species to exploit. Frost and Langenheim (1974) recognized pioneer, pre-climax, and climax stages in their analysis of the development of the Oligocene Pueblo Nuevo reef of Mexico, and Mesoella *et al.* (1970) distinguished pioneer deep-water assemblages (with predominantly doming-massive corals) from later shallower-water stages (with predominantly branching corals) in the Pleistocene reefs of Barbados.

Some insight into the methodology that has governed much of the geological research into reef succession can be gained from a recent review by Walker and Alberstadt (1975). These authors analysed the development of eight ancient reef masses in detail (see their fig. 2) and found that four vertical zones are generally present. A basal stabilization stage (or zone) represents the initial preparation of the substrate for reef growth; in Palaeozoic reefs this typically involved the accumulation of small, localized mounds of echinoderm calcarenite. Reef-building organisms then preferentially colonized the early, stabilized mounds and a framework was gradually built up. In both the colonization and diversification stages there is a marked increase in the numbers and variety of both reef-building and reef-dwelling taxa. Implicit in this analysis is the assumption that each stage 'prepares the ground' for the succeeding stage. The various organisms of each stage grow and develop, and collectively alter the environment in such a way that in time they will be replaced by others more suited to exploit the newly created habitats. This is the classic autogenic succession of Tansley (1935). In the final stage, or domination zone, one or a few taxa predominate. The change from the diversification to domination zones is often abrupt and it may be that the latter represents the sudden imposition of allogenic (i.e. external) factors such as water turbulence.

Walker and Alberstadt (1975) are in no doubt that the stages in their analysis are interconnected and part of an irrevocable process of community development. They state (1975, p. 243; see also their fig. 1) that during the first three stages there is a steady increase in the following community parameters: the number of species, growth habit diversity, stratification, food-web complexity, and other organism interrelations. These increases lead to 'homeostasis by diversification' and result in the development of highly biologically accommodated assemblages.

Thus we arrive at a mechanism of fossil reef succession that may be termed 'community controlled'. The physical environment is progressively modified by the reef community to produce an orderly and, to some extent, predictable sequence of species. Reef biomass and diversity gradually increase and in time a stabilized, highly integrated community is produced. This mechanism seems to correlate well with many observed fossil reef successions.

SOME THEORETICAL CONSIDERATIONS

The community-control concept has had a profound influence on the study of ecological succession. Originating with works of Clements (1916, 1936), the idea of succession as an orderly process of community development has pervaded ecological thinking ever since (see, e.g., Olson 1958; MacArthur and Connell 1966; Margalef 1968; Odum 1969; and Whittaker 1975). However, appealing as this community-control theory may be, it must be pointed out that it is based as much on inference and analogy as it is on fact and observation. Few studies to date have actually documented an orderly replacement of early successional species by members of later communities (Drury and Nisbet 1973; Connell and Slatyer 1977). It has also been shown that the theory runs contrary to the principle of natural selection. If an early species 'prepares the ground' for a later one, it will be actively creating an environment that is more favourable to the survival of another species than to itself. Natural selection must act on all species including successional ones (Colinvaux 1973; Drury and Nisbet 1973). Much of the evidence for the progressive development of stabilized, highly integrated communities can in fact be shown to be no more than the result of the passage of time.

Biomass increases through succession because it takes time to grow, and diversity must progressively increase because a succession will always start with zero species. Far from representing a homeostatic equilibrium, the end point of succession may simply be the running-out of available species (Gleason 1926).

It has long been recognized (see, e.g., Egler 1954) that nearly all species in a successional sequence are either present before the sequence starts or appear shortly afterwards. Ecological succession may in fact be no more than a sequential expression of conspicuousness (Drury and Nisbet 1973, p. 352). Those species appearing early in a succession are simply those that are common and well dispersed, whereas those appearing later are less common and have slower mechanisms of dispersal. In time, progressively rarer species should colonize any given area (see, e.g., Gleason 1926; MacArthur and Wilson 1967; Goulden 1969).

This recognition of ecological succession as a sequential expression of conspicuousness represents a fundamental shift in emphasis from a consideration of properties of the community as a whole to those of the individual. Modern successional theory is now based on the fundamental roles of physical stress on individuals and competition between individuals for available resources (Colinvaux 1973; Drury and Nisbet 1973; Horn 1974, 1975, 1976). It is important for early successional species to be able to invade openings, grow, and mature quickly. For a time these early species will be able to suppress competitors, but they will be replaced eventually by later colonists that live longer and grow to greater sizes. This replacement of early colonists with 'opportunistic' strategies by later ones with 'equilibrium' strategies is well documented (Colinvaux 1973; Drury and Nisbet 1973; Horn 1974). It is analogous to MacArthur and Wilson's (1967) replacement of 'r selected' species by 'K selected' ones (see Odum 1969; Colinvaux 1973).

In an important review of successional mechanisms, Connell and Slatyer (1977) have stressed that the interactions of plants (or sessile animals) with herbivores, predators, and pathogens can also be of critical importance to the course of succession. Connell and Slatyer propose three simple models. The facilitation model is equivalent to that of community-control outlined above. It assumes that only certain early successional species can colonize a particular site. These then grow and modify the environment so that it is more suitable for colonization by later successional species. In the second and third models (the tolerance and inhibition models, respectively) any species, including those typical of late succession, may be able to colonize an area. The tolerance model is essentially similar to the mechanism of sequential conspicuousness in that later species are simply late arrivals or those that took longer to grow. They are tolerant species adapted to grow at lower levels of resources than early successional species. The work of Loucks (1970) suggested that the tolerance model may have widespread application, but Connell and Slatyer (1977) could find little evidence to support it.

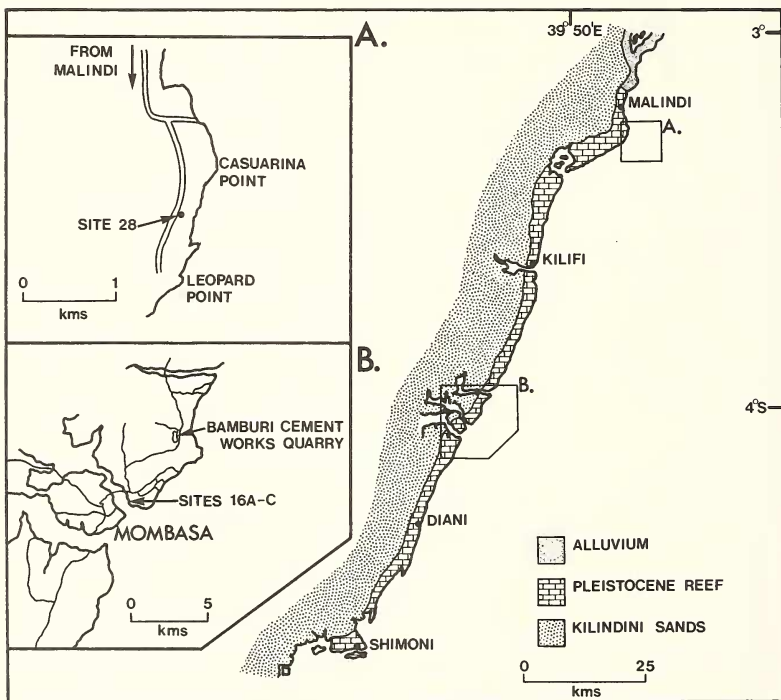
In the third (inhibition) model there are no faunal replacements until damage (by physical disturbances, predation, etc.) creates an opening in the community. Any available species can then invade the opening; there is no need for the ground to be prepared or for the replacing species to be more tolerant. As early successional species are by nature shorter-lived ones, they will in time gradually be replaced by the longer-lived late successional species. Ecological successions from short-lived to long-lived species are commonly observed (Connell and Slatyer 1977). An important point to note here is that, in the facilitation and tolerance models, species are progressively eliminated through competition, but in the inhibition model they are eliminated by the action of physical disturbances, herbivores, predators, and pathogens.

We may conclude from this brief review that more emphasis should be placed on elucidating the role of individuals in ecological successions. Geologists in particular should concentrate less on establishing vertical zones or stages and more on examining individual species. Detailed analysis of species abundance and distribution patterns at successive levels through a reef should reveal much about colonization strategies, relative growth rates, and competitive interactions. Direct evidence of interspecific interference and overgrowths may also be found, and in time it should be possible to establish the successional roles of the principal frame-building organisms in any reef tract. Only then will it be possible to test adequately models such as those outlined above.

Finally, it is important to bear in mind that most recent successional theories relate to the re-establishment of a pre-existing community in a relatively constant environment. In other words they deal with what are essentially secondary successions. On the other hand, many reef successions are concerned with the establishment of a new community (often in an inconstant environment) and as such are primary successions. Important differences can be expected between primary and secondary successional mechanisms.

FIELD AREA AND METHODS

The Pleistocene reef forms a narrow but continuous strip along the Kenya coast between Malindi and Shimoni (text-fig. 1). Uniform, unfossiliferous sands (the Kilindini Sands) are continuously exposed along its inner margin and there is evidence, especially in the Mombasa region, that these sands underlie (and thus pre-date) the main reef deposits. Whereas much of the early Pleistocene



TEXT-FIG. 1. A simplified geological map of the Kenya coast. Insets A and B show the locations of Sites 28 and 16A-C, respectively. The sites studied at the northern end of the Bamburi Cement Works quarry are shown in text-fig. 3.

history of the Kenya coast was dominated by the accumulation of sands (mainly of continental origin) on a low coastal plain, much of the later history was dominated by periods of reef growth. Detailed mapping along various parts of the coast has shown the reef stratigraphy to be complex, and as yet no precise chronology of reef-building events can be established. It is thought likely that the majority of exposures can be referred to a single (though complex) depositional event which took place during the last Interglacial (c. 120 000 years BP) (Crame 1977). However, limited exposures of lower reef limestone units occur in a number of areas, most noticeably Bamburi (text-figs. 1 and 2) and between Diani and Shimoni (text-fig. 1). In the Mombasa area the main reef limestones are 6–8 m thick. They thicken eastwards to form cliffs of 10–12 m, and thin westwards to 2–3 m at the junction with the Kilindini Sands (text-fig. 1).

It is also as yet impossible to present a detailed facies model of the Pleistocene reef, owing to uncertainty as to the contemporaneity of the various depositional units and lack of information in certain key areas. Enough is known, however, from those reconstructions that have so far been made (Crame 1977), to speculate on the general form of the reef.

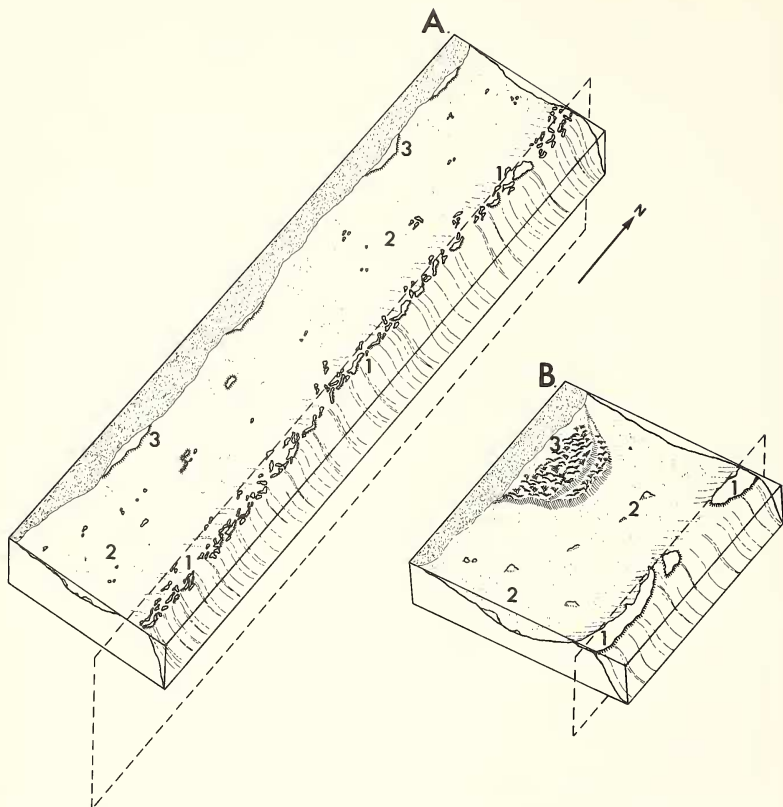
The present-day reef platform along the Kenya coast is primarily an erosional feature (pers. obs.; see also Crossland 1902, 1903), and what was the outer half of the Pleistocene reef has now been largely removed by marine erosion. Remnants of the seaward extremities are preserved, however, in certain headlands and creek mouths and these are typically composed of thick, branching *Acropora* assemblages. This outer *Acropora* facies probably represents the remnants of a series of small, isolated, and coalescing reef masses that developed along the reef margin close to the shelf edge (text-fig. 2A). Under constant wave attack, these outer reefs would have been dominated by thick algal crusts and shallow-water, high-energy *Pocillopora* and *Acropora* assemblages.

There is little extensive frame growth over much of the inner half of the Pleistocene reef, and it is clear that this was essentially a back-reef region supporting only small reef clumps and isolated coral mounds (text-fig. 2). Occasionally, however, larger reefs were able to develop in this back-reef region, perhaps opposite the more substantial gaps in the outer reef cluster. The *Acropora* bank exposed in the north and west faces of the Bamburi Portland Cement Works quarry may well be one such reef (text-figs. 1 and 2B).

Vertical sections through the Kenya Pleistocene reef can be studied in a series of quarries, road-cuts, and cliff-lines from Malindi to Shimoni (text-fig. 1). Over forty such sections have now been examined in detail as part of a long-term project to investigate the internal structure and development of a major reef tract. From these, a series of sections through dense coral framework was selected for an analysis of reef development in terms of ecological succession. In making this selection, an effort was made to choose sites that reflected reef growth in a variety of environments.

Sedimentary and faunal evidence suggests that all the areas of frame coral growth described in this work accumulated under conditions of relatively constant water depth. Bedding planes are rare in the surrounding matrix calcarenites, and there are no distinct horizons of either stunted or flat-topped coral colonies to suggest the sudden imposition of very shallow-water conditions. There is some evidence of a terminal shallow-water event in the Pleistocene reef limestones along some parts of the Kenya coast, but this occurs at a level well above the top of any of the sites studied.

Vertical quadrats, varying between 5 and 35 m in width and between 2 and 5 m in height, were marked out on each of the sections studied. A detailed map was then drawn, at a scale of 1:10, of each quadrat, and particular attention was paid to determining the shape and attitude of individual coral colonies. To this end, hachuring and shading were employed, and the resulting sketch of each section is in fact a three-dimensional picture. This method is of course more time consuming than merely plotting colony outlines or using symbols, but it was found to expedite greatly the subsequent analysis of the stages of reef development. Other features marked on the maps include minor sedimentary structures and patches of rubble. During construction of some of the maps, a number of loose coral colonies were encountered. If it seemed likely that a loose coral had grown in close proximity to where it now lay and had merely toppled over from its life position, it was included in the map and subsequent analysis. If, however, a coral showed signs of severe abrasion and had obviously been transported, it was regarded as reef rubble and excluded from the analysis.



TEXT-FIG. 2. A three-dimensional model of the Kenya reef during the last Interglacial. A. The reef tract between Malindi and Shimoni. 1. Outer reef wall: composed of isolated and coalescing reef masses. 2. Back-reef region: predominantly small, isolated coral mounds and patches. 3. Small fringing reefs: developed at intervals along the sandy shore. B. A generalized reconstruction of the reef in the region of the Bamburi Portland Cement Works quarry. 1. Outer reef wall. 2. Back-reef region: scattered coral mounds on a sandy-calcareous substrate. 3. An *Acropora*-dominated bank. In both A and B the portion of the block lying to the right of the dashed rectangle has now been removed by marine erosion. The width of both blocks is approximately 5 km.

Very few corals fell into the latter category. Wherever possible, the base of a quadrat was placed on or close to a stratigraphic break, to investigate the pioneer coral faunas that had colonized bare surfaces. A particularly useful datum to use in this context is the top of the underlying sands formation.

The resulting maps were analysed at half-metre vertical intervals. Numbers of coral species and individuals were determined for each interval, and an estimate made of individual coral colony size. For the latter, the outline of the colony, as projected onto the plane of the paper, was taken to represent a vertical section through it. The area of this outline was then calculated using a simple grid-overlay technique. The resulting figure, the number of squares on the grid occupied by a planar section through the colony, has been termed the Importance Value of the coral. The species diversity of each half-metre interval was calculated using the Shannon-Weaver information theory index:

$$H' = - \sum_{i=1}^S p_i \ln p_i$$

(where H' is the information content of the sample, S is the total number of species, and p_i is the proportion of the total sample belonging to the i^{th} species). It should be noted that the validity of using an information theory index such as this to measure biological diversity has been seriously questioned (see, e.g., Hurlbert 1971; Horn 1974; Goodman 1975; May 1975). However, of all the various measurements that incorporate the relative abundances of species, the Shannon-Weaver is the one most widely used. It has been consistently employed in the study of recent coral assemblages (Loya 1972, 1976c; Porter 1972a, b; Grigg and Maragos 1974) and its continued usage is advocated here in the hope that it may eventually lead to a detailed comparison of coral species diversity patterns in a range of contrasting reef environments.

The function H' is influenced by both numbers of species in the sample (S) and the evenness of their distribution among the individuals in the sample (Lloyd and Ghelardi 1964). A greater number of species will increase the species diversity and so too will a more even (or equitable) distribution among the species. Equitability (J') can be measured in a number of ways (Pielou 1975), one of the simplest being:

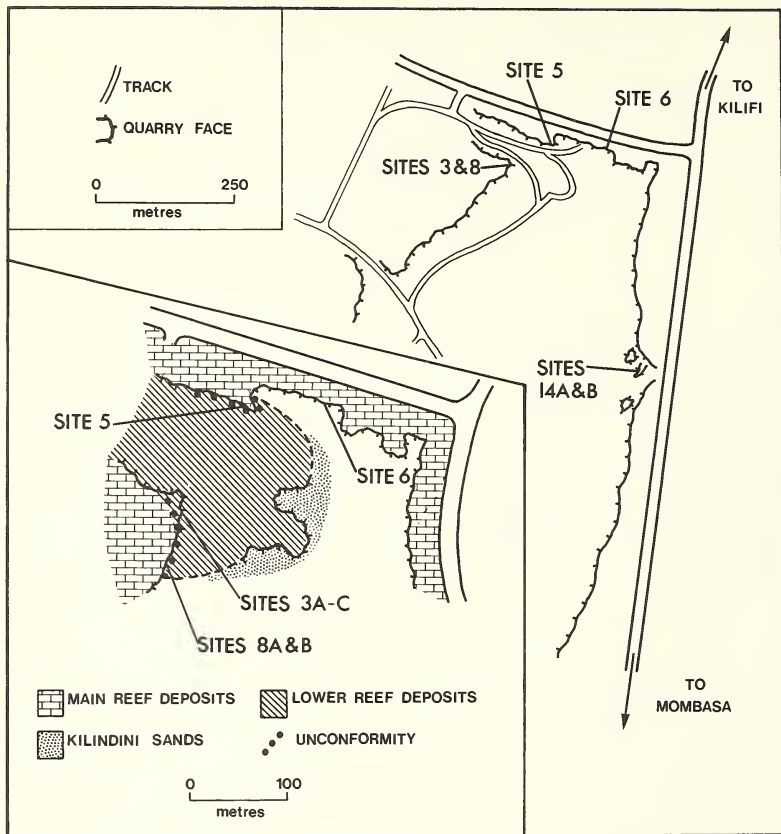
$$J' = \frac{H'}{H_{\max}}$$

(where $-H_{\max} = \log S$ is the maximum value of H' , which occurs when all species in the sample are equally distributed among the individuals).

The degree of preservation of the corals is often such as to prevent accurate identification to the species level. In a number of instances the fine detail of calice structure and surface ornament has either been removed (by weathering or diagenetic solution) or obscured (by encrusting organisms or sediment). Consequently it has not been possible to identify certain types of coral beyond rather broadly defined groups. An explanation of the grouping used in this study is contained in the Appendix.

SUCCESSION ON SHALLOW-WATER, UNCONSOLIDATED SUBSTRATES

At the northern end of the Bamburi Portland Cement Works quarry, a lower series of reef deposits is separated from the main reef by a marked unconformity (text-fig. 3). These lower deposits developed directly on the lower sands formation in what were, at least initially, very shallow-water conditions. High angle cross-bedding, large quartzose pebbles, and patches of coarse coral-mollusc debris all occur along the line of the sands-reef transition zone and suggest that at times beach-type conditions prevailed. Directly above this transitional layer, low, irregular domes and patches of coral framework, measuring up to 2.5 m (horizontal) by 2 m (vertical), are developed. These framework areas alternate with comparatively barren patches of sandy calcarenite that support only small composite coral mounds and isolated coral colonies. Three quadrats were studied in this area



TEXT-FIG. 3. Sites studied at the northern end of the Bamburi Portland Cement Works quarry. The inset is a geological sketch-map showing the approximate distribution of the principal depositional units.

(Sites 3A, 3B, and 3C, text-fig. 3) through three separate framework structures. Sites 3B and 3C are adjacent and separated by 4 m of barren calcarenite from Site 3A. The base of the quadrat at all three sites was placed at the top of the sandy transitional layer, and it is believed that the structures described developed at approximately similar elevations above the sea floor.

Similar mounds of coral framework are exposed in cuttings along the Malindi-Leopard Point road (text-fig. 1, inset A). These mounds, although of similar height, have slightly greater linear dimensions and are set closer together. They contain some extremely high densities of corals, and



TEXT-FIG. 4. Part of the quadrat studied at Site 3A. Key: 1. lower sands formation, 2. early doming-massive faviids, 3. small clumps of *Galaxea fascicularis*, 4. thick, encrusting layers of matrix, 5. later faviids, 6. a large colony of *Favia stelligera*, 7. a small clump of *Acropora* and *Pocillopora*. Horizontal and vertical grid interval: 0.5 m.

altogether this would appear to have been an area of more prolific coral growth. The mounds developed on a sandy substrate, but their bases are nowhere clearly exposed. It is believed that they form part of the main reef limestones and thus post-date the reef deposits at Site 3.

Succession at Site 3A (text-figs. 4 and 6) (quadrat size: 4 m (horizontal) \times 1.5 m (vertical))

The most important initial colonizer on the sands at this site is *Galaxea fascicularis* (Lamarck). It occurs in small, spiky (fasciculate) clumps that are often totally encased in sandy matrix. Small doming-massive faviids also occur within the lowest half-metre (text-fig. 4) but there are virtually no branching types such as *Acropora* or *Pocillopora*. *G. fascicularis* is known to be a particularly efficient sediment-remover that thrives at the present day in shallow, sandy environments (Marshall and Orr 1931). In this particular instance, low mounds formed by the coalescing spiky clumps must have given important initial relief to the local reef structure (text-fig. 4).

Also prominent in the first and second intervals are doming-massive faviids such as *Favia*, *Favites*, *Goniastrea*, and *Platygyra* (text-figs. 4 and 6). These are all robust types capable of withstanding the forces of shallow, turbulent seas (e.g. Wells 1954; Yonge 1973) and, by virtue of their large polyps, they are also efficient sediment-removers (e.g. Marshall and Orr 1931; Maxwell 1968; Mergner and Scheer 1974). The hillocky growth form of *Favia stelligera* (Dana) is typical of shallow, turbulent environments (Wells 1954; Wijsman-Best 1972, 1974) and large colonies such as that seen in the second interval of the quadrat (text-fig. 4) must have considerably promoted early

topographic development of the reef. Associated with the increase in topographic complexity in the second and third intervals is the occurrence of a number of small branching corals belonging to the families Acroporidae and Pocilloporidae (text-figs. 4 and 6).

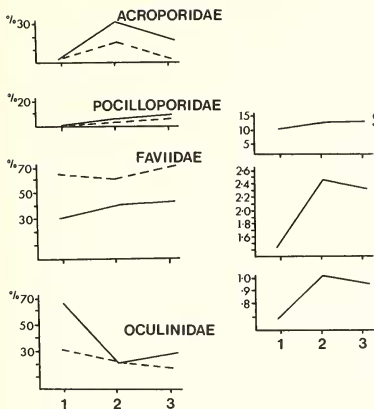
Succession at Site 3B (text-fig. 6) (2.5×2 m)

The vertical sequence in this quadrat is essentially similar to that seen at Site 3A. Low mounds formed by clumps of *Galaxea fascicularis* predominate in the first two intervals, together with doming-massive faviids (of which *Favia* sp. gp. 1 is particularly common). The graphs (text-fig. 6) document the progressive demise of these large-calice faviids and the rise of both the Acroporidae and

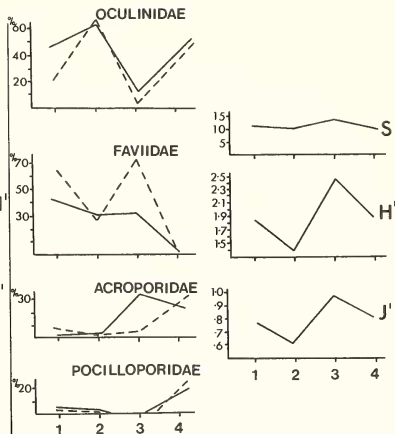


TEXT-FIG. 5. The quadrat studied at Site 3C. Key: 1. lower sands formation, 2. massive *Porites*, 3. small clumps of *Pocillopora*, 4. thick, platy *Acropora*, 5. mixed *Acropora-Pavona* assemblage, 6. thick-branching *Acropora*, 7. layers of matrix. Horizontal and vertical grid interval: 0.5 m.

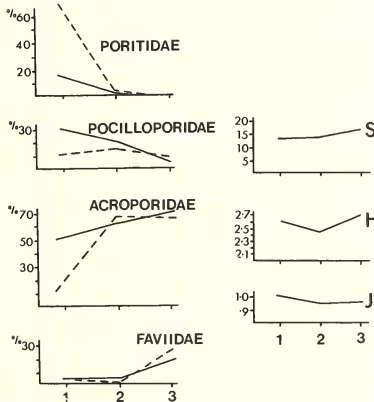
SITE 3A



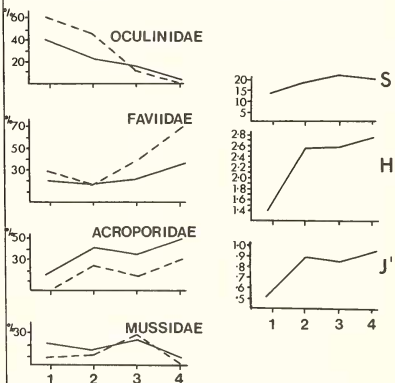
SITE 3B



SITE 3C



SITE 28



TEXT-FIG. 6. Coral trends and diversity trends for Sites 3A, 3B, 3C, and 28. The coral trends are given as percentages of the total coral fauna occupied by the principal Families at successive half-metre intervals. They are documented in terms of both numbers of specimens (solid line) and Importance Values (dashed line). Diversity trends are given in terms of numbers of species (S), the Shannon-Weaver information index (H'), and Pielou's measure of equitability (J'). The figures on the horizontal axes represent successive half-metre intervals above the base of the quadrat.

Pocilloporidae in the later stages. It would appear that, once a certain elevation had been attained, species of both *Acropora* and *Pocillopora* were able to colonize the area. The trends for *G. fascicularis* (Oculinidae, text-fig. 6) show pronounced fluctuations.

Succession at Site 3C (text-figs. 5 and 6) (2×1.5 m)

In marked contrast to Sites 3A and 3B, the initial coral assemblage developed on the sands at this site is composed of small clumps of *Pocillopora* and several large colonies of massive *Porites* (text-fig. 5). However, small, bushy species of *Pocillopora*, similar to those seen here, are known to thrive in environmentally unpredictable areas such as reef flats (e.g. Mayor 1924; Crossland 1928; Manton 1935), and Marshall and Orr (1931) have shown that *P. bulbosa* (? = *P. damicornis* (Linnaeus)), like *G. fascicularis*, is capable of withstanding large influxes of sediment. Species of massive *Porites* are hardy too, and in many parts of the Indo-Pacific province have been observed to colonize soft (generally sandy) substrates (e.g. Manton 1935; Umbgrove 1947; Maxwell 1968; Maragos 1974a).

The early *Pocillopora*-*Porites* assemblage is replaced in the second and third intervals by a thick framework of branching, encrusting, and doming-massive corals (text-fig. 5). Species of *Acropora*, especially *A. palifera* gp. 1, *A. palifera* gp. 3, and *Acropora* sp. gp. 8, predominate, together with several thick-branching colonies of *Pavona clavus* (Dana) and the occasional massive faviid. Both the Poritidae and the Pocilloporidae decrease in importance up the quadrat, as the Acroporidae and Faviidae increase (text-figs. 5 and 6).

Diversity trends through succession at Sites 3A, 3B, and 3C

There is obviously no progressive increase in species diversity through succession at these three sites (H' values, text-fig. 6). At various levels all three quadrats show pronounced drops in diversity and it would seem that this is largely due to the dominance exerted by certain coral species. When resources (especially available habitat space) become limiting, fewer species will be able to coexist and the competitively successful ones, such as the faster-growing types, will become dominants. Grigg and Maragos (1974) have suggested that dominance in coral faunas is brought about by competitive interactions such as exploitation or pre-emption (i.e. rapid growth), interference, or predation (see Lang 1971, 1973). It is probable that large faviids exerted a dominant influence in the third interval at Site 3A, *G. fascicularis* in the second and fourth intervals at Site 3B, and large species of *Acropora* in the second interval at Site 3C. Concomitant with the rise of these dominants there is in each case a marked fall in diversity.

It might be expected that the evolution of dominance will affect the equitability component of species diversity rather more than the species richness component. Under normal circumstances the general trend for a J' curve should be a progressive increase through succession as the individuals present become more evenly distributed among the various species. A sudden influx of individuals, however, associated with the rise of a dominant species, would seriously disrupt this process and cause a sharp fall in J' values. It is indeed the case that at all three sites the form of the J' curve closely resembles that of the H' curve (text-fig. 6).

Succession at Site 28 (text-figs. 1, 6, and 7) (5×2 m)

The quadrat at this site was positioned in the centre of a low mound measuring just over 10 m across and ranging in height from 2.5 m in the centre to 1 m at either end. The lowest interval of the quadrat is dominated by thick intergrowths of *G. fascicularis* and large doming-massive faviids (principally *Platygyra* sp. and *Favia* sp. gp. 1) (text-fig. 7), and again there is evidence that these coral types flourished in a shallow, sandy environment. The mussid, *Lobophyllia*, and a few small colonies of platy *Acropora* are the only other corals present in the first interval (text-figs. 6 and 7). In the middle and upper levels of the second interval there is an abrupt change to a rich *Acropora*-faviid assemblage (text-fig. 7). Within this assemblage there are platy and branching acroporids (*Acropora* sp. gps. 2, 3, 6, and 7), doming-massive and encrusting faviids (*Favia*, *Platygyra*,



TEXT-FIG. 7. Part of the quadrat studied at Site 28. Key: 1. dense clumps of *Galaxea fascicularis*, 2. *Platygyra* sp., 3. *Favia* sp. gp. 1, 4. *Lobophyllia*, 5. platy-encrusting *Acropora*, 6. *Diploastrea heliophora*, 7. *Leptoria phrygia*, 8. mixed *Acropora* assemblage, 9. *Leptastrea* sp. gp. 2. Horizontal and vertical grid interval: 0.5 m.

Goniastrea, *Hydnophora*, and *Echinopora*), and a few scattered colonies of *Galaxea* and *Lobophyllia*.

Diversity rose abruptly upon establishment of the initial mound but then rose more gradually through the rest of the quadrat (H' values, text-fig. 6). Clearly, the *Galaxea*-faviid assemblage provided a topographic prominence that was subsequently colonized by a wide variety of other coral types.

This vertical sequence is very similar to that seen at Sites 3A and 3B. That a more substantial coral assemblage subsequently developed on the *Galaxea*-faviid base at this site suggests that there were subsequently slightly deeper or calmer-water conditions in this area.

SUCCESSION ON DEEPER-WATER, UNCONSOLIDATED SUBSTRATES

Quadrats studied at two sites in the Bamburi Portland Cement Works quarry (Sites 6 and 14, text-fig. 3) record the establishment and subsequent development of coral assemblages on soft substrates in deeper-water environments (the estimated depth at both sites being in the 10-30 m range).

The coral assemblage at Site 6 is dominated by two distinctive elements: large platy colonies of *Acropora* which have shallow, saucer-shapes in cross-section, and are often stacked in tiers, and

thick-branching clumps of *A. palifera* (= *A. palifera* gp. 1). It closely resembles reef front terrace assemblages developed at depths of about 10 m on both the Great Barrier Reef (e.g. Maxwell 1968, fig. 77) and Tutia Reef, Tanzania (Talbot 1965).

Immediately to the north and east of the second site (Site 14, text-fig. 3), patches of a plain, uniform calcarenite are exposed that contain no corals other than the tiny ahermatypic forms *Heterosammia* and *Heterocyathus*. Both of these occur at the present day on sheltered, sandy bottoms at depths generally between 10 and 30 m (Goreau and Yonge 1968; Wijzman-Best 1972; Rosen 1972; Pichon 1974). At Site 14 itself, however, a rich assemblage of corals is exposed in a complex knoll measuring some 15–20 m across in its longest dimension and 2.5–3 m in height in the centre. The quadrat at Site 14A is oriented in an approximately north–south direction through the knoll, and that at Site 14B in an east–west direction. The two quadrats are separated by a horizontal distance of 5 m. It is believed that similar-sized knolls developed sporadically in the region of what is now the eastern margin of the Bamburi Portland Cement Works quarry, together with large, isolated coral colonies (among which *Porites* sp. gp. 2 are common). These knolls and corals grew up from what was essentially a level, sandy bottom.



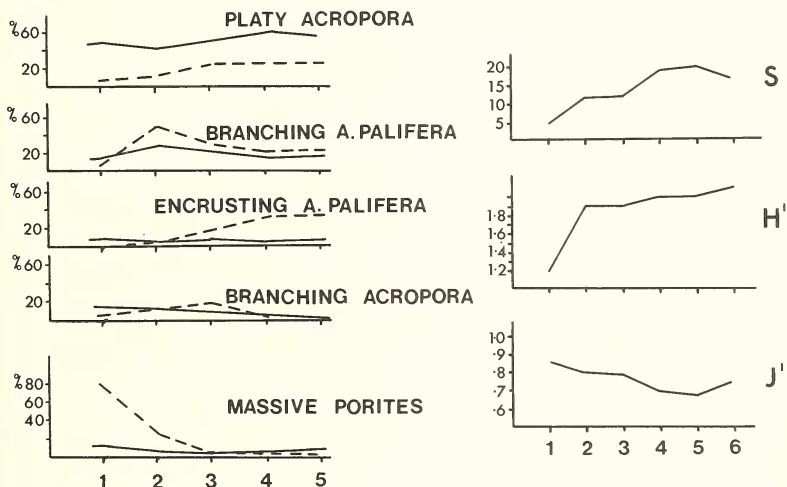
TEXT-FIG. 8. Part of the quadrat studied at Site 6. Key: 1. sparsely populated *Halimeda* calcarenite, 2. thick-branching *Acropora palifera*, 3. platy *Acropora*, 4. massive *Porites*, 5. massive-encrusting *A. palifera*, 6. *Pocillopora* sp., 7. branching rubble. Horizontal and vertical interval: 0.5 m.

The deposits at Sites 6 and 14 are part of the main reef limestones and are thought to rest directly on the lower Kilindini Sands unit. They represent deeper-water facies that developed along the northern and eastern flanks of the Bamburi quarry, respectively. Contemporaneously, shallower-water *Acropora*-dominated assemblages developed in the region of the western margin of the quarry (Crame 1977, fig. 38).

Succession at Site 6 (text-figs. 8 and 9) (25×2.5 m)

The vertical sequence revealed in the quadrat at this site is rather different from those previously described. Corals are less abundant, there are no extensive areas of frame, and no dramatic faunal replacements occur (text-figs. 8 and 9). Species of *Acropora* predominate, and the principal coral elements, platy *Acropora* species and thick-branching *A. palifera*, remain relatively constant (at least in terms of numbers of colonies present) throughout the quadrat. There is, however, a gradual increase in both coral abundance and diversity (text-figs. 8 and 9). In the three highest intervals further species of *Acropora* are encountered, together with occasional colonies of types such as *Pocillopora* sp., *Porites* sp. gp. 1, *Porites* sp. gp. 2, and a few small faviids. The process of ecological succession at this site has clearly been one of the very gradual colonization of a barren substrate, followed by an incremental build-up of both coral species abundance and diversity.

SITE 6



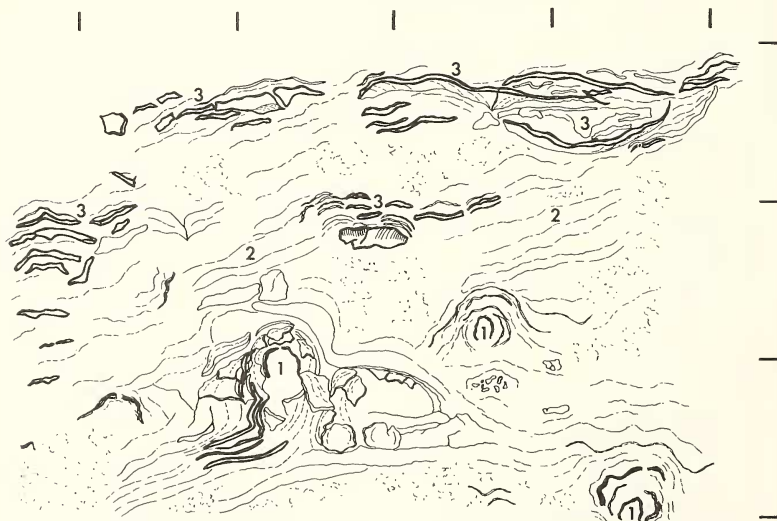
TEXT-FIG. 9. Coral trends and diversity trends for Site 6. The coral trends are given as percentages of the total coral fauna occupied by the principal coral groups at successive half-metre intervals. They are documented in terms of both numbers of specimens (solid line) and Importance Values (dashed line). Diversity trends are given in terms of numbers of species (S), the Shannon-Weaver information index (H'), and Pielou's measure of equitability (J'). The figures on the horizontal axes represent successive half-metre intervals above the base of the quadrat.

After a sharp initial rise, the H' curve then increases only comparatively slowly through the rest of the quadrat (text-fig. 9). It will be noted too, from text-fig. 9, that whereas the species richness (S) curve increases from the first to the fifth interval, the equitability curve (J') steadily decreases. The reason for this is that, in the early stages of succession, the addition of further species (i.e. increasing the species richness, S) has the effect of increasing the diversity value H' for the whole assemblage. At later stages, however, the addition of further species tends to decrease the value of H' , since these later arrivals are rarer in occurrence and will thus upset the equitability (J'). The net effect of these two trends is to produce an H' curve that increases sharply initially but then levels off (text-fig. 9; compare also Loya 1972, fig. 9). In the sixth interval the S values fall for the first time and the J' values rise. This probably marks the end of species immigration into the area and the establishment, for the first time, of an equilibrium assemblage.

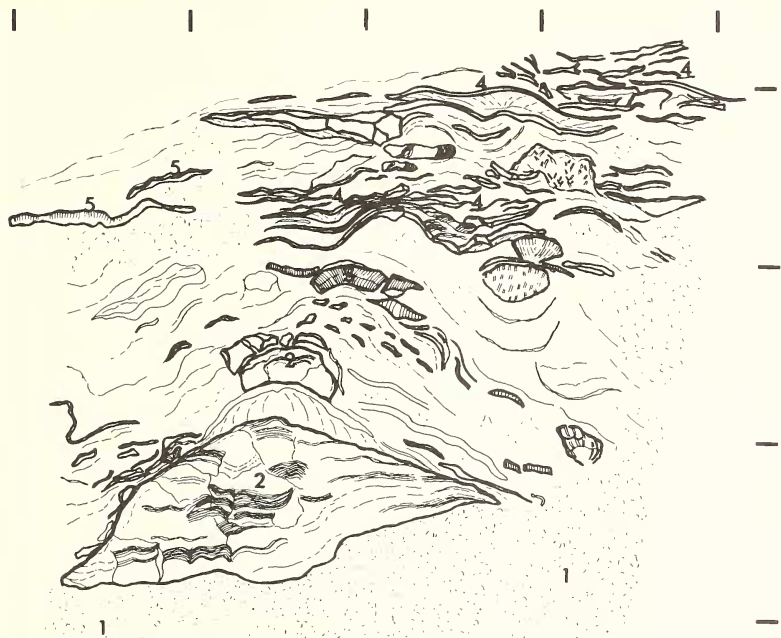
Succession at Site 14 (text-figs. 10 and 11) (14A: 5×1.5 m) (14B: 2.5×1.5 m)

Conspicuous at the base of the quadrat at Site 14A are a number of small, ball-like structures (text-fig. 10). These are in fact small coral colonies that have been coated with thick layers of encrusting algae and coral. Coral cores within the structures include small, massive heads of *Porites* sp. gp. 2, *Favia* sp. gp. 1, and *Platygyra* sp., and doming-encrusting *Montipora* sp. Later encrusting corals are predominantly *Pachyseris* sp. and *Montipora* sp.

In the second and third intervals the ball structures are replaced by thick layers of sediment and thinner platy-encrusting layers of coral (text-fig. 10). At this particular site *Montipora* sp. is the commonest of these later platy corals, but there are also a few small colonies of *Pachyseris* sp. It



TEXT-FIG. 10. Part of the quadrat studied at Site 14A. Key: 1. coral domes covered with layers of encrusting algae and coral, 2. platy layers of sediment, 3. layers of platy-encrusting coral, mostly *Montipora* sp. Horizontal and vertical grid interval: 0.5 m.



TEXT-FIG. 11. The quadrat studied at Site 14B. Key: 1. plain calcarenite, 2. massive *Porites*, 3. encrusting *Goniastrea pectinata*, 4. *Pachyseris* sp., 5. platy *Montipora* sp. Horizontal and vertical grid interval: 0.5 m.

would thus appear that the early ball-like structures formed an initial protruberance on the sea floor that was subsequently covered by thick, platy layers of sediment and coral.

At Site 14B the initial relief was provided by a single, large, doming-massive colony of *Porites* sp. gp. 2, which grew directly on the fine calcarenite substrate (text-fig. 11). Later corals, including another massive *Porites* and a thick, doming-encrusting *Goniastrea pectinata* (Ehrenberg), accentuated the initial dome formed by the *Porites* and a distinct hummock must have been produced on the sea floor. This feature was subsequently covered by a succession of platy-encrusting coral layers (principally *Pachyseris* sp.) (text-fig. 11).

As light intensity decreases with depth on a reef, so competition must increase among corals to occupy space in the light. A good strategy for such competing corals is to have a high surface to volume ratio (i.e. to be platy or sheet-like in form; e.g. Goreau 1963; Barnes 1973). Unfortunately, a reef structure cannot be built entirely out of platy corals for they would be unable to lift it significantly above the sea floor and it would have little intrinsic strength. It is suggested that the successions seen at Sites 14A and 14B are, in essence, the sequence by which any deeper-water knoll reef might be expected to develop. Initially, a solid foundation is formed, and then, when sufficient relief has been developed, the mound is colonized by platy corals.

Quantitative analysis of the faunal trends was not possible at Sites 14A and 14B as many of the platy corals are too thin for the areas of vertical sections through them to be accurately measured. In many instances too, it is impossible to determine the number of separate colonies that are present.

SUCCESSION ON HARD SUBSTRATES

The prominent unconformity between the main-reef and the lower-reef deposits at the northern end of the Bamburi Portland Cement Works quarry (text-fig. 3) is subaerial in origin. This means that the early part of the main reef in this area developed on a hard substrate, in marked contrast to almost all the other areas investigated. The unconformity is well exposed at Site 8 (text-fig. 3), where immediately above it there is a thin, sandy-rubby layer containing both coral fragments and iron-stained quartz pebbles. Two quadrats with their bases resting directly on this transitional layer were studied at Site 8. They are separated by a horizontal distance of 2 m and it is believed that



TEXT-FIG. 12. The quadrat studied at Site 8A. Key: 1. transitional sandy-rubby layer, 2. doming *Favia* sp. gp. 1, 3. doming *Goniastrea retiformis*, 4. layers of matrix, 5. mixed *Acropora-Pocillopora-Porites* assemblage, 6. a later-colonizing *Astreopora horizontalis*, 7. platy *Acropora*. Horizontal and vertical grid interval: 0.5 m.

the structures described within them developed synchronously and to similar levels above the substrate. A third quadrat studied at Site 5 (text-fig. 3) has its base at an estimated height of 1–1.5 m above the sandy transitional layer. It is judged that the structure described within this quadrat attained similar dimensions to those at Sites 8A and 8B, but that it occupied a slightly higher position on the gently sloping eroded surface of the Lower Reef Series. The main reef in the vicinity of both Sites 5 and 8 is predominantly an *Acropora* facies (Crame 1977, fig. 38), with small branching and platy-based *Acropora* colonies being especially prominent.

Succession at Site 8A (text-figs. 12 and 14) (2.5 × 1.5 m)

At the base of this quadrat there are two small but prominent mounds, each of which is cored by a doming-massive faviid (one is *Favia* sp. gp. 1, the other *Goniastrea retiformis* (Lamarck)) (text-fig. 12). As before, it is thought that these were probably tolerant corals able to thrive in a high-energy, sand-transporting environment. They would be both resistant to strong water movements and capable of removing considerable sediment influxes. On recent reefs, both *G. retiformis* and many large-calice species of *Favia* frequently adopt such pioneering roles in shallow, sandy environments (e.g. Mergner and Scheer 1974; Maragos 1974a; Wijsman-Best 1974).

Thick layers of sandy matrix eventually encased the two early colonizing doming-massive corals (text-fig. 12) to form a low but distinct mound. This feature was subsequently colonized by a variety of corals, including *Pocillopora* sp., several species of branching *Acropora*, *Porites* sp. gps. 1 and 2, *Astreopora* sp., and *Galaxea fascicularis*. Fairly rapidly, however, *Acropora* species become dominant, and by the third interval they are by far the most important type (text-figs. 12 and 14). Corymbose species (predominantly *Acropora* sp. gp. 3) and small forms with platy bases (*Acropora* sp. gp. 7) are particularly common.

Succession at Site 8B (text-fig. 14) (2.5 × 1.5 m)

Three colonies at the base of this quadrat also have doming-massive forms, but are different species from those seen at the base of 8A. Two of the colonies are species of the caryophyllid genus, *Gyrosmilina*, and the third is *Porites* sp. gp. 2. Little is known about the habits of *Gyrosmilina*, but its large meandrine calices probably reflect an efficient sediment-clearing mechanism and this, together with its robust growth form, would make it a potentially good early colonizer of bare surfaces.

In this quadrat the pioneers are replaced even more dramatically by species of *Acropora* than at Site 8A. Small, branching colonies of *Acropora* dominate the second and third intervals, with corymbose species (*Acropora* sp. gps. 1–3) and horizontally branching sprays (*Acropora* sp. gp. 6) being especially common. The striking rise in the Acroporidae at the expense of all the other coral families is clearly illustrated in text-fig. 14.

Succession at Site 5 (text-figs. 13 and 14) (4 × 1.5 m)

The coral assemblage in the lower levels of the quadrat at this site is dominated by two distinctive elements: large, doming-massive colonies of *Porites* sp. gp. 2 and comparatively small colonies of branching *Acropora* (text-fig. 13). The latter include forms with distinct platy bases and some small sprays, but most characteristic are a number of corymbose colonies of *Acropora* sp. gps. 2 and 3. Towards the top of the second interval and in the third interval, however, there is a pronounced change. The coral fauna here is dominated by branching forms (with corymbose *Acropora* being especially common) and doming-massive forms are virtually absent (text-fig. 13). It would seem then, that after the early establishment of a mixed coral fauna, the branching corals, and in particular the relatively faster-growing species of *Acropora* (see, e.g., Stoddart 1969 for a summary of coral growth rates), replaced nearly all the other coral types and dominated the reef. *Acropora* sp. gps. 2 and 3 are the dominant species in the third interval (text-figs. 13 and 14), but there are also a few small colonies of types such as *A. palifera* (platy and encrusting forms), *Montipora*, *Porites* sp. gp. 1, and *Galaxea fascicularis*.



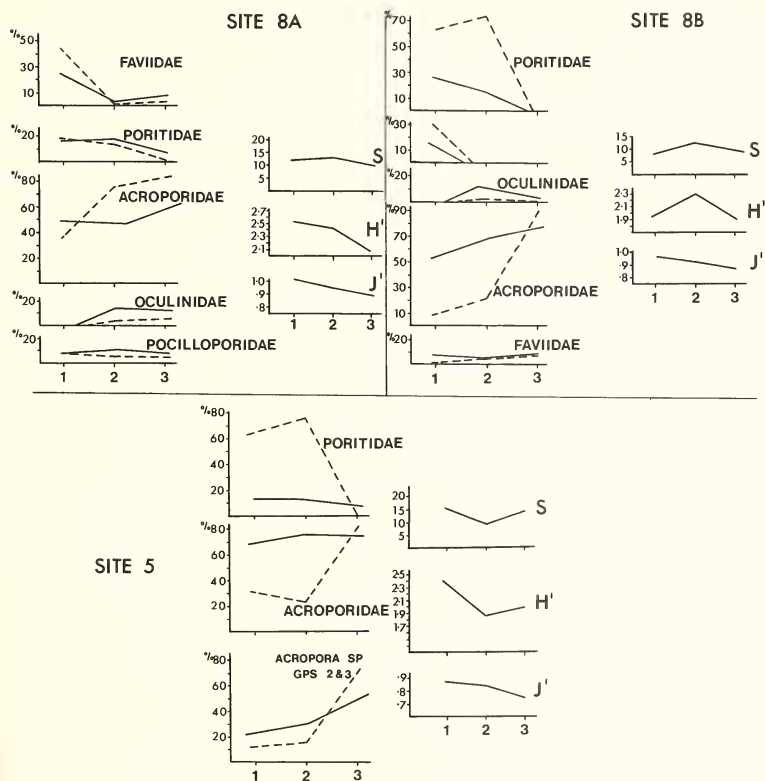
TEXT-FIG. 13. Part of the quadrat studied at Site 5. Key: 1. massive *Porites*, 2. mixed stands of *Acropora*, 3. dense clumps of corymbose *Acropora*, 4. platy *Acropora*, 5. *Galaxea fascicularis*, 6. layers of matrix. Horizontal and vertical grid interval: 0.5 m.

Both Gravier (1910) and Mayor (1924) suggested that the faster-growing corals, and in particular species of *Acropora*, would in time displace the doming-massive forms on a reef, and Connell (1973, 1976), by direct observation of fixed quadrat sites, has actually observed this process in operation. Indeed, were it not for the fact that many slower-growing species can protect themselves from being overgrown by extruding mesenterial filaments and killing off the encroaching edge of a competitor (Lang 1971, 1973; Connell 1976), competition would be much more rapid, and the very existence of numerous slow-growing shallow-water corals would be seriously jeopardized.

Diversity trends through succession at Sites 8A, 8B, and 5

The fall in diversity throughout the quadrat at Site 8A and the sharp drop from the second to the third interval at 8B (H' curves, text-fig. 14) almost certainly reflect the strong dominance exerted by species of *Acropora*. The trend at Site 5 is less easily explained in these terms, as the establishment of the dominant corymbose *Acropora* assemblage in the third interval is actually accompanied by an increase in diversity (H' curve, text-fig. 14). However, the diversity value obtained for the second interval is an extremely low one, as two very large *Porites* colonies occupy much of the available space (text-fig. 13). The progressive imposition of dominance is mirrored in the continual fall in J' values through succession at all three sites (text-fig. 14).

Sedimentary and faunal evidence suggests that shallow-water conditions (probably in the 2–10 m depth range) prevailed at both Sites 8 and 5. Once again, it would appear that the early evolution of dominance can be linked to reef initiation and development in a shallow-water environment.

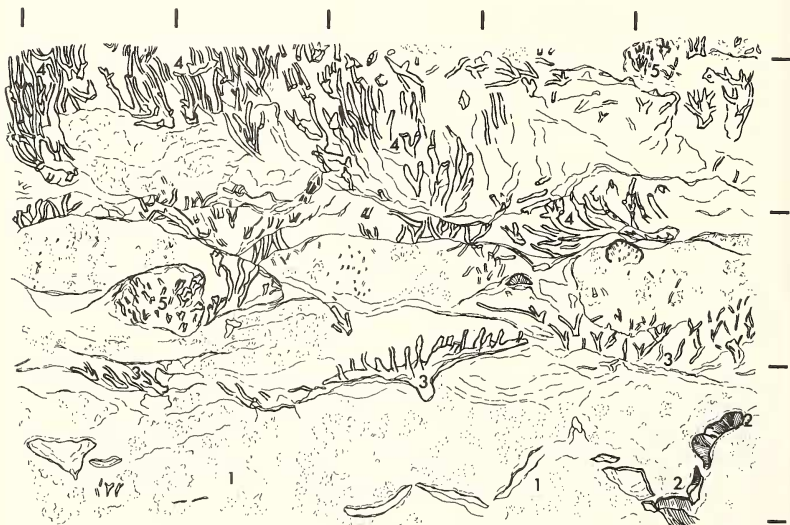


TEXT-FIG. 14. Coral trends and diversity trends for Sites 8A, 8B, and 5. The coral trends are given as percentages of the total coral fauna occupied by the principal Families and coral groups at successive half-metre intervals. They are documented in terms of both numbers of specimens (solid line) and Importance Values (dashed line). Diversity trends are given in terms of numbers of species (S), the Shannon-Weaver information index (H'), and Pielou's measure of equitability (J'). The figures on the horizontal axes represent successive half-metre intervals above the base of the quadrat. N.B. The trend for the Acroporidae at Site 8A is considerably influenced by the large later-colonizing *Astreopora*.

SUCCESSION IN A STAGSHORN *ACROPORA* AREA

Although stagshorn species of *Acropora* (= *Acropora* sp. gp. 4 in this study—see Appendix) are common constituents of many shallow-water coral assemblages, they are rather rare in the Kenya Pleistocene reef. However, a stagshorn-dominated assemblage is exposed near the mouth of the Nyali Creek in a 500 m strip of cliff-line along the eastern bank (Site 16, text-fig. 1). Here, a prominent band of stagshorn *Acropora*, 1–1.75 m thick, occurs sandwiched between lower and upper layers of sandy calcarenite (0.5–0.75 m and 2–2.5 m thick, respectively). The former contains patches of coral rubble and isolated, *in situ* coral colonies, but the latter is barren. The stagshorn *Acropora* band has a sandy matrix, a well-defined base, and a remarkably level upper surface. It is thought that it developed as a thick bank of branching coral on a gently sloping sands substrate. Indeed, it is likely that the Pleistocene reef in this area developed directly on the lower sands formation, for the latter is well exposed a short distance inland in the Nyali Quarry. Traced inland, the stagshorn *Acropora* passes successively into branching rubble and then back-reef patch facies (Crame 1977, fig. 56). The three quadrats studied at this site (16A–C, text-fig. 1) are separated by horizontal distances of 12 and 20 m, respectively. Their bases were placed at the top of the lower sandy calcarenite and they record reef development at equivalent levels.

Strictly speaking, these quadrats should of course have been included under the heading of succession on shallow-water, unconsolidated substrates, but the assemblages here are so different from all other *Acropora* assemblages studied, and the vertical trends so striking, that they are deemed worthy of consideration within a separate category.



TEXT-FIG. 15. Part of the quadrat studied at Site 16A. Key: 1. lower sandy layer, 2. early faviids, 3. early colonies of stagshorn *Acropora* (*Acropora* sp. gp. 4), 4. later colonies of stagshorn *Acropora*, 5. branching *Porites* (*Porites* sp. 1). Horizontal and vertical grid interval: 0.5 m.

Succession at Site 16A (text-figs. 15 and 17) (10×1.5 m)

The visual impression of progressive domination by stagshorn *Acropora* (text-fig. 15), is amply confirmed by the analysis (text-fig. 17). In the initial half-metre interval, where coral growth is rather patchy and irregular, small stagshorn colonies are established on the sandy substrate, but so too are corymbose *Acropora* colonies (*Acropora* sp. gp. 3), branching poritids (chiefly *Porites* sp. gp. 1), doming-massive faviids, and several small colonies of *Galaxea fascicularis*. All these forms, however, with the exceptions of *Acropora* sp. gp. 3 and *Porites* sp. gp. 1, become insignificant in the second interval, which is predominantly occupied by stagshorn colonies (text-fig. 17). The latter have increased in both number and size, and clearly, by a process of lateral extension across the substrate, have monopolized nearly all the available habitat space. Domination by stagshorn *Acropora* is virtually complete by the third interval (text-figs. 15 and 17).

Although they do occur at depth on some reef fronts, stagshorn species of *Acropora* are more typical of shallow, sheltered environments on reef flats and in lagoons (e.g. Wells 1954; Davies *et al.* 1971; Stoddart 1973; Pichon 1974). Stagshorn species grow quickly (Vaughan and Wells 1943; Goreau 1961), and once established rapidly cover all available ground space (Braithwaite 1971; Maragos 1974b; Connell 1978).

It can be concluded that the reef at Site 16A developed on a flat to gently sloping bank in shallow, open waters. In all probability conditions were similar to those described by Braithwaite (1971) for a reef on the north-east side of Cerf Island (Seychelles), where a prolific stagshorn growth was recorded on a broad, gently sloping bank in depths of no more than 1–2 m.

Succession at Site 16B (text-figs. 16 and 17) (2×1.5 m)

The first interval of this quadrat is dominated by stagshorn *Acropora*, which has clearly established itself on, and grown across, the sandy substrate (text-fig. 16). Other corals that grew directly on the sandy basal layer include *Galaxea fascicularis*, *Acropora hyacinthus* (digitate form—see Appendix), and *Porites* sp. gp. 1. In the second interval the stagshorn maintains its over-all importance (text-figs. 16 and 17), but it has not been able to dominate to the extent that it did at the equivalent level at Site 16A. A range of other coral types (all branching in form) are still found in this interval; these include, *Porites* sp. gp. 1, *A. humilis* (included in *Acropora* sp. gp. 1), and *A. palifera* gp. 4. There is a marked change, however, from the second to the third interval, with the mixed branching assemblage of the former being replaced in the latter by an assemblage dominated by just two coral types, stagshorn *Acropora* and *Porites* sp. gp. 1.

When the trends of individual coral types are plotted out (text-fig. 17), it becomes apparent that branching *Porites* (*Porites* sp. gp. 1) has gradually increased in importance as the reef structure grew, principally at the expense of stagshorn *Acropora*. Small digitate species of *Acropora*, at least in terms of numbers of colonies present, remained relatively constant (text-fig. 17).

Succession at Site 16C (text-fig. 17) (2.5×1.5 m)

Coral growth in the initial interval of this quadrat is totally dominated by stagshorn *Acropora* (text-fig. 17). At least three colonies have grown directly off the underlying sands and, by the base of the second interval, a thick mesh of branching coral has been formed. Half-way up the second interval, however, a number of other coral types suddenly appear. These include corymbose *Acropora* (*Acropora* sp. gp. 3), *Pocillopora* sp., and branching *Porites* (*Porites* sp. gp. 1), each of which rests on, and is in turn covered by, stagshorn *Acropora*. As in the quadrat at Site 16B, the mixed coral assemblage of the second interval is replaced by one in the third interval in which only two coral elements (in this instance stagshorn *Acropora* and corymbose *Acropora*) are prominent.

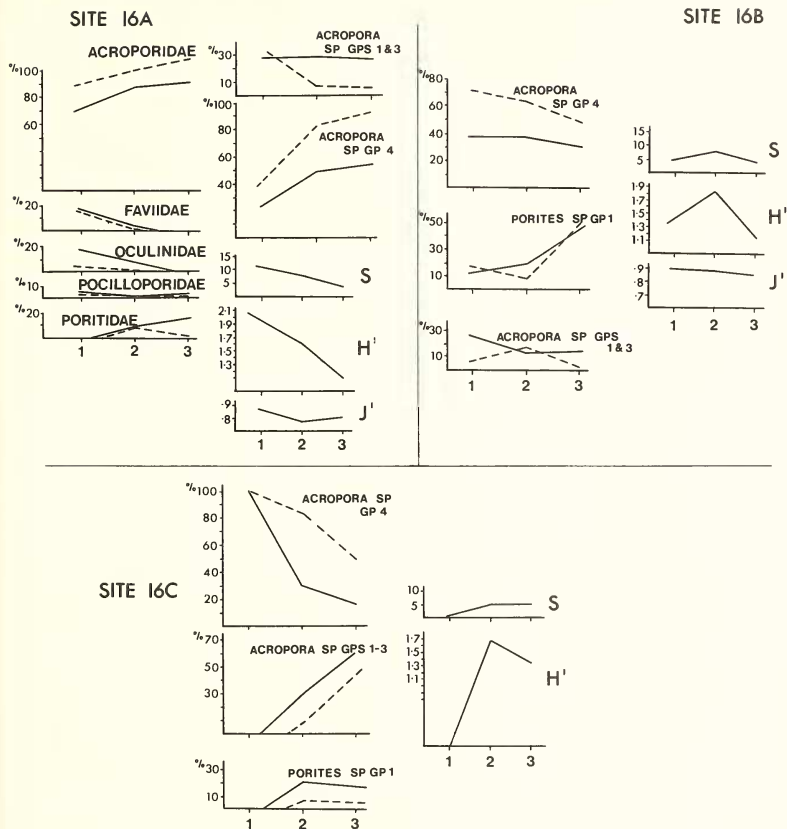
The graphs of the trends for individual coral types (text-fig. 17) clearly show how the corymbose species of *Acropora* (*Acropora* sp. gps. 1–3) gradually increased in importance as the reef structure grew, whereas the stagshorns gradually decreased. It seems that, just as *Porites* sp. gp. 1 displaced stagshorn *Acropora* through the quadrat at Site 16B, so corymbose *Acropora* species displaced it at this site.



TEXT-FIG. 16. The quadrat studied at Site 16B. Key: 1, lower branching layer, 2, stagshorn *Acropora*, 3, branching *Porites*, 4, *A. humilis* (*Acropora* sp. gp. 1), 5, loose, rubbly material. Horizontal and vertical grid interval: 0.5 m.

Diversity trends through succession at Sites 16A, 16B, and 16C

The diversity trend for the quadrat at Site 16A reflects the progressive domination of the site by stagshorn *Acropora*. There is a moderately high H' value for the initial coral assemblage, but this falls steeply in the subsequent intervals as the stagshorn becomes increasingly abundant (text-fig. 17). At the other two sites there are low initial H' values due to the early dominance by stagshorn, but higher values in the second interval, where mixed branching assemblages occur (text-fig. 17). In the third interval, however, in both instances, diversity drops again as dominance is re-exerted. The reason for the relaxation in dominance in the middle interval at these two sites is not known for certain, but it may be that an environmental disturbance, such as an abrupt shallowing or storm damage, disrupted the early stagshorn assemblage and allowed other branching types to colonize the area. This may well be one instance of an extrinsic disturbance actually promoting an increase in species diversity.



TEXT-FIG. 17. Coral trends and diversity trends for Sites 16A, 16B, and 16C. The coral trends are given as percentages of the total coral fauna occupied by the principal Families and coral groups at successive half-metre intervals. They are documented in terms of both numbers of specimens (solid line) and Importance Values (dashed line). Diversity trends are given in terms of numbers of species (S), the Shannon-Weaver information index (H') and Pielou's measure of equitability (J'). The figures on the horizontal axes represent successive half-metre intervals above the base of the quadrat. N.B. Because of the exceptionally low diversity values in the first two intervals, J' values have not been calculated for Site 16C.

DISCUSSION

The various successional trends described in this study have been summarized in Table 1. For each of the four categories of reef environment, three stages of development are shown. It should be emphasized that these stages have been selected on a somewhat arbitrary basis to aid comparison of the various successional mechanisms. No hard and fast boundaries exist between them.

Community-control (or obligatory) succession

In view of some of the arguments presented in the introduction, it is perhaps surprising to find a number of instances of community-control succession in the Kenya Pleistocene reef (see categories 1, 3, and 4i, Table 1). This type of succession falls within Connell and Slatyer's (1977) facilitation model and is equivalent to Horn's (1976) obligatory succession model. At Sites 3A, 3B, 3C, and 28,

TABLE 1. Successional trends in the Kenya Pleistocene reef

1. SHALLOW-WATER, UNCONSOLIDATED SANDS

- | | | |
|---|--|---|
| i. Early domes and mounds formed by clumps of sediment-tolerant corals such as <i>Galaxea fascicularis</i> and <i>Pocillopora</i> , and doming-massive types such as <i>Porites</i> sp. gp. 2, <i>Favia</i> sp. gp. 1, <i>Platygyra</i> , and <i>Goniastrea</i> . | ii. The early mounds extend up into relatively calmer, clearer water and are colonized by the faster-growing branching and platy-encrusting corals (mostly species of <i>Acropora</i>). | iii. A thick framework is formed, composed of branching and platy-encrusting types, but with few doming-massive corals. |
|---|--|---|

2. SHALLOW-WATER, FIRM SAND SUBSTRATE

- | | | |
|--|---|--|
| i. Bare sand is colonized by a mixed assemblage of stagshorn <i>Acropora</i> colonies and types such as <i>Goniastrea retiformis</i> and <i>Galaxea fascicularis</i> . | ii. Stagshorn <i>Acropora</i> increases dramatically in both size and numbers of colonies; nearly all other coral types are excluded. | iii. A thick framework of stagshorn <i>Acropora</i> is formed which is broken only in places by small stands of coral types such as corymbose <i>Acropora</i> and branching <i>Porites</i> . |
|--|---|--|

3. SHALLOW-WATER, HARD SUBSTRATE

- | | | |
|---|--|--|
| i. Doming-massive corals such as <i>Porites</i> sp. gp. 2, several faviids, and <i>Gyrosmlia</i> colonize the substrate and are subsequently covered by layers of sediment and encrusting corals. | ii. Early mounds extend up into relatively calmer, clearer water and are colonized by branching and encrusting corals (principally species of <i>Acropora</i>). | iii. A thick framework of coral is formed, with species of <i>Acropora</i> being especially prominent. |
|---|--|--|

4. DEEPER-WATER, SOFT SUBSTRATES

- | | | |
|---|---|---|
| i. Colonization of the bare (sand) substrate by doming-massive corals (e.g. <i>Porites</i> , <i>Favia</i> , and <i>Platygyra</i>), some of which are subsequently covered by thick layers of encrusting algae. | ii. Colonization of the early mounds by platy and platy-encrusting corals (especially <i>Montipora</i> and <i>Pachyseris</i>). | iii. Domination of the mounds by thick stands of platy corals (especially <i>Pachyseris</i> and <i>Montipora</i>). |
| i. Slow colonization by a small number of platy and thick-branching <i>Acropora</i> species (in a <i>Halimeda</i> -dominated environment). | ii. Incremental build-up of further <i>Acropora</i> species. | iii. Eventual formation of a rich <i>Acropora</i> assemblage in which large platy and thick-encrusting species are especially prominent; a few small stands of other branching and encrusting types are also present. |

early mounds were formed from a combination of sediment-tolerant and massive coral types such as *Galaxea fascicularis*, *Pocillopora*, *Porites* sp. gp. 2, *Favia* sp. gp. 1, *Platygyra*, and *Goniastrea*. It is assumed that as soon as the tops of these mounds penetrated relatively calmer, clearer water, they were rapidly colonized by faster-growing types, and in particular by branching and platy-encrusting acroporids. These early colonizing corals have all been recorded in similar pioneer roles in recent reef environments. *Pocillopora* is a prodigious early colonizer in Panamá (Glynn *et al.* 1972), Hawaii (Grigg and Maragos 1974; Stimson 1974), and the Red Sea (Loya 1976a, b), and *Galaxea fascicularis* frequently occurs in isolated stands in shallow, sandy areas (e.g. Rosen 1972). Many species of massive faviid and *Porites* have also been observed as pioneers on sandy bottoms throughout the Indo-Pacific province (Manton 1935; Umbgrove 1947; Wells 1954; Maxwell 1968; Wijsman-Best 1972; Maragos 1974a; Mergner and Scheer 1974).

Similar patterns of obligatory succession were observed at Sites 8A and 8B. Here, in what was again thought to have been a shallow-water environment, early doming-massive corals gave the local reef structure a firm foundation and elevated it sufficiently above the rubbly sea floor to allow more sensitive corals (especially species of *Acropora*) to become established in strength. Massive corals are also replaced by branching coral types at Site 5. A number of large *Porites* colonies occur low down in the quadrat at this site, but these are replaced at successively higher levels by numerous small, branching colonies (especially corymbose *Acropora*).

A consistent picture emerges, then, of obligatory succession in shallow-water environments being characterized by an early assemblage of sediment-tolerant corals (some or all of which are doming-massive in form) which is subsequently replaced by an assemblage that is typically rich in branching and platy-encrusting acroporids (i.e. categories 1 and 3, Table 1). Both Mayor (1918) and Manton (1935) recorded living branching *Acropora* species extending across massive faviids, and Talbot (1965, p. 446) suggested that certain shallow-water species of *Acropora* were actually smothering massive *Porites* colonies on Tutia Reef (Tanzania). In a more general way, a number of other authors have indicated that reef development is typified by an initial phase in which massive corals predominate, followed by a subsequent phase of branching and platy-encrusting species (e.g. Umbgrove 1947; Goreau 1959; Mesolella *et al.* 1970; Frost and Langenheim 1974). Braithwaite *et al.* (1973) have shown that the Pleistocene Aldabra Limestone is characterized by a preponderance of doming-massive forms at its base but branching forms at higher levels.

Obligatory succession also occurred in the deeper-water environments of Sites 14A and 14B. In both instances, early assemblages of doming-massive corals cored mounds that were subsequently covered by thick layers of sediment and colonized by platy-encrusting coral types such as *Pachyseris* and *Montipora*. This situation is analogous to that seen on many recent reef fronts (especially at depths in excess of 10 m) where large sheets of platy-encrusting coral frequently grow over a massive foundation (e.g. Goreau 1959).

Although obligatory succession is obviously an important mechanism of reef development, it must be pointed out that it is essentially restricted to the earliest stages of reef development on a bare substrate. It is hard to find evidence of obligatory sequences at higher levels and it is likely that, once a framework has been established, further succession is governed principally by the more cryptic influences of interspecific competition and extrinsic disturbances.

Random, non-directional trends

Apart from the early obligatory sequences, there is little evidence of clear-cut directional trends in the sections studied. Only very generalized stages of reef development can be recognized (Table 1), and among the principal frame-building species there appear to be no more than two broad categories of colonizing strategy (early and later colonizers, Table 2). Even the community-control (or obligatory) sequences are far from constant in terms of species composition, for we have seen how there is a variety of pioneers on both soft and hard substrates, and many different species that can subsequently replace them. Quite why succession should appear to be so unstructured and haphazard is at first perplexing, but a plausible explanation can perhaps be found by recourse to theoretical arguments put forward in the introduction.

TABLE 2. Ecological roles of the principal frame-building corals in the Kenya Pleistocene reef

	3A	3B	3C	28	6	14A	14B	8A	8B	5	16A	16B	16C
<i>Pocillopora</i> sp. gp. 1			E										
sp. gp. 2			E										
sp.	L	L	E	L				L			E		
<i>Acropora</i> sp. gp. 1													
sp. gp. 2				L	L								
sp. gp. 3	L	L	L	L	L			L	L	L	E-L		L
sp. gp. 4											E-L	E-L	E-L
sp. gp. 6									L				
sp. gp. 7	L	L	L	L	L			L	L	L			
sp. gp. 8					L				L				
<i>palifera</i> gp. 1			L		E-L			L					
gp. 2			L	L				L		L			
gp. 3			L		L								
gp. 4												L	
<i>Astreopora horizontalis</i> de Blainville				L				L					
<i>Montipora</i> sp.				L		E-L	L						
<i>Pavona clavus</i> (Dana)			L										
<i>Pavona</i> sp.			L										
<i>Pachyseris</i> sp.						L	L						
<i>Porites</i> sp. gp. 1										L	L	L	L
sp. gp. 2			E	E-L	E	E	E-L	E	E				
<i>Alveopora</i> sp.									L				
<i>Favia stelligera</i> (Dana)	E	E		L									
<i>Favia</i> sp. gp. 1		E		E		E		E					
<i>Goniastrea retiformis</i> (Lamarck)	E							E			E		
<i>Goniastrea pectinata</i> (Ehrenberg)							L						
<i>Goniastrea</i> sp.				L									
<i>Platygyra lamellina</i> (Ehrenberg)	E			E									
<i>Platygyra</i> sp.	E	E		E		E							
<i>Leptoria phrygia</i> (Ellis and Solander)				E-L									
<i>Hydnophora microconos</i> (Lamarck)				L									
<i>Diploastrea heliophora</i> (Lamarck)				L									
<i>Leptastrea</i> sp. gp. 2				L									
<i>Echinopora</i> sp.	L	L											
<i>Galaxea fascicularis</i> (Lamarck)	E	E		E						L	E		
<i>Acanthastrea echinata</i> (Dana)				L									
<i>Lobophyllia corymbosa</i> (Forskål)				E									
<i>Gyrosmilina</i> sp.									E				

Key: E—early colonizer; L—later colonizer; E-L—both early and later colonizer.

In Connell and Slatyer's (1977) inhibition model there is no ecological succession until an extrinsic disturbance damages or destroys one or a small number of established residents: any available species may then colonize the newly created opening. Thus, extrinsic influences such as storm damage, predation, or the effect of pathogens will govern the course of ecological succession. Such influences are known to be widespread on coral reefs (Grassle 1973; Connell 1976, 1978; Loya 1976c) and it is likely that they will occur on a time scale shorter than that required for intrinsic community development (Drury and Nisbet 1973, p. 358). Golley (1977, p. 329) has summarized the situation succinctly when he states, "... the response of the community to disturbance through succession is more significant than the possible orderly sequence of communities in space or time. The essence of succession may well be response not pattern."

In a recent review of species diversity in tropical rain forests and coral reefs, Connell (1978) has argued that corals (and trees) are very generalized in their resource requirements. He could find no evidence to suggest that corals had partitioned either their habitats or trophic resources to the extent that would be necessary to bring about the very high observed diversities. Coral reefs (and rain forests) are not the highly integrated, co-evolved species complexes that they have traditionally been assumed to be. Disruptions (physical disturbances, predation, etc.) are probably so frequent that equilibrium conditions are rarely attained. The continually fluctuating conditions prevent any one species or group of species from monopolizing resources and thus maintain a high species diversity. They also actively promote the continual formation of clearings in reefs and forests that permits the widespread occurrence of inhibition succession. Random sequences can thus be expected, *a priori*, to be the rule rather than the exception on established coral reefs.

Competition in early succession

It is unlikely, however, that all ecological successions will be entirely random, non-directional processes governed only by the nature and extent of extrinsic disturbances. The inhibition model of succession relates primarily to secondary successions on well-established reefs. At earlier stages of reef development interspecific competition must surely occur, for there will almost certainly be a distinct phase of replacement of early colonizers by later arrivals.

There is as yet insufficient data on the life histories, dispersal powers, and competitive abilities of most hermatypic corals to enable them to be classified as either *r* or *K* strategists. Pocilloporids, however, are one group that consistently show *r* strategist characters (Loya 1976a, b), and at Site 3C *Pocillopora* is certainly a prominent early colonizer. Doming-massive faviids and *Porites* are also important pioneers (Table 2), but their large size and comparatively slow growth rates preclude them from being considered as *r* strategists in the strict sense. However, it is interesting to note that on reef flats in the Gulf of Eilat (Red Sea), small encrusting faviids and *Porites* adopt opportunistic roles (Loya 1976c). *Galaxea fascicularis*, a prodigious early colonizer, occurs as numerous small, spiky colonies and is widely dispersed throughout the Kenya Pleistocene reef. It is here provisionally classified as an *r* strategist along with the pocilloporids.

We have already discussed how pioneer coral assemblages tend to be rapidly colonized and dominated by faster-growing branching and platy-encrusting corals. At Site 5, for example, an early *Porites*-dominated assemblage is replaced by a thick corymbose *Acropora* assemblage, and at Sites 8A and 8B early mounds, based on doming-massive corals, were rapidly colonized by a mixture of branching and platy-encrusting *Acropora*. At Site 16, stagshorn *Acropora* was seen to be an extremely effective competitor, rapidly outgrowing other early colonizers to form large, monospecific stands. Clearly, in any competitive hierarchy between shallow-water reef species, branching and platy-encrusting species (and especially acroporids) are likely to predominate. Instances have been recorded of massive corals resisting overgrowth (e.g. Connell 1976, p. 52), but as a general rule we can assume that the slower-growing massive corals will rank lower in competitive ability to most branching and platy-encrusting types (cf. Connell 1976, table 1). Besides stagshorn *Acropora* (*Acropora* sp. gp. 4), other species likely to rank high in competitive hierarchies within the Kenya Pleistocene reef are *Acropora* sp. gps. 3 and 7, *A. palifera* gp. 2, and *Porites* sp. gp. 1 (Table 2). It may be concluded, therefore, that the principal short-term successional trend on many shallow-water reefs (i.e. those in approximately the 2–10 m depth range) will be rapid domination by branching and platy-encrusting corals, and in particular by acroporids.

In deeper-water environments, such as at Sites 14A and 14B, branching and platy-encrusting corals will in some cases be competitively subordinate to certain coral types with large platy and sheet-like colonies (such as *Pachyseris* and *Montipora*). Although not necessarily faster-growing, such colonies are more efficient at occupying space in the light and thus absorbing more of the incident light energy.

Longer-term trends

We may also expect to find some pattern to the later phases of reef development. Inhibition succession is characterized by a gradual introduction of longer-lived species and thus we might expect to see the gradual domination of a reef by large, massive corals: Grime (1977, p. 1189) has shown that a consistent feature of vegetation succession is the incursion of plants of greater size. In broad terms, we should expect a progressive replacement of small colonies (of all types) by large, massive ones. The former will be initially more successful in securing space, but in time they will be replaced by more durable, massive forms. It should be emphasized that this is a much slower, longer-term process than any of the other successional replacements outlined above. In both coral reefs and tropical forests, the gradual rise to dominance of assemblages of large species probably involves time-spans of several hundreds of years.

Some evidence of a trend towards eventual domination by large, massive colonies comes from Sites 6 and 28. At Site 6, massive encrusting colonies of *A. palifera* become increasingly important at higher levels (text-fig. 8), and at Site 28 the reef mound is capped by several large, doming-encrusting faviids (text-fig. 7). The large size and gradual rise to dominance of corals such as these are features suggestive of **K** strategies.

Long-term domination by slower-growing doming-massive corals can also be predicted by considering a relationship between temporal sequences of species and spatial sequences along stress gradients. Drury and Nisbet (1973, p. 358) have pointed out that species prominent in the early stages of succession (opportunists or **r** selected species) are characteristic of high-stress sites on environmental gradients, whilst those prominent in the later stages (equilibrium or **K** selected species) are characteristic of the low-stress end. Now it is well known that corals occur on recent reefs in distinct zones (see, e.g., the review by Rosen 1975) and that the principal cause of the zonation is response to an environmental stress gradient. Consequently, might not the coral zonation patterns we see on recent reefs reflect a potential temporal zonation? In his scheme for Indo-Pacific reefs, Rosen (1975) has established the following five zones (or associations) on the basis of faunal response to a stress gradient of water movement: (i) Calcareous algae, (ii) *Pocillopora*, (iii) *Acropora*, (iv) Faviids, (v) *Porites*. The zones intergrade from the shallow-water (high-energy) Calcareous algae zone to the deep-water (low-energy) *Porites* zone. If left to develop uninterrupted, an Indo-Pacific reef would therefore be expected to show a temporal sequence of zones grading from Calcareous algae to *Porites*. Thus in time *Pocillopora* assemblages might be replaced by *Acropora*-dominated assemblages and the latter by massive faviid and poritid assemblages. Massive corals can indeed resist overgrowth by faster-growing species (Lang 1971, 1973; Connell 1976), and over an extended period of time it would be possible for them to eventually dominate a reef. However, such long-term transitions have yet to be convincingly demonstrated in either fossil or recent reefs.

Diversity through succession

A long-standing tenet of ecology has been that complex tropical ecosystems are inherently stable. However, powerful theoretical arguments have recently been advanced against this stability-diversity concept (e.g. May 1973) and it is now thought that tropical high diversity is as much the product of a constantly fluctuating environment as it is of extensive resource partitioning in a benign environment (e.g. Connell 1978). If small, localized disturbances are continually occurring on a reef, we can expect no consistent pattern of species diversity change through succession. Clearly, the process of incorporating further species into the reef will be continually interrupted.

In this study four generalized categories of diversity change through succession have been recognized.

i. Diversity increase in a constant environment

At Sites 6 and 28 species diversity continues to increase through succession (H' values, text-figs. 6 and 9). In both instances there is an abrupt early rise in diversity followed by smaller increases at higher levels. The sharp increase in the species richness component (S) at both sites

in the early stages most likely represents an initial phase of species immigration, whilst the increase in J' values in the highest intervals (text-figs. 6 and 9) reflects an increase in species evenness. An early rise in species richness followed by an increase in species evenness is probably the mechanism by which coral species diversity is continually built up in any constant reef environment.

ii. Diversity decrease in a constant environment

At Site 16A diversity falls continually through succession (H' values, text-fig. 17) as the original mixed assemblage is progressively dominated by stagshorn *Acropora*. There is no evidence of a break in the faunal sequence at this site and thus it would appear to be a genuine instance of succession being accompanied by a reduction in species diversity. Similar reductions in diversity caused by dense overgrowths of branching *Acropora* have been recorded on several recent reefs (e.g. Connell 1978, pp. 1304–1305; Talbot 1965, p. 447).

iii. Diversity increase in a fluctuating environment

At Sites 16B and 16C diversity rises sharply from the first to the second interval (H' values, text-fig. 17) when early dense stands of stagshorn *Acropora* are replaced by mixed coral assemblages. It is thought likely that localized extrinsic disturbances (such as damage by predators or a storm, or the effects of a low spring tide) created openings in the stagshorn stands at these sites that subsequently allowed other coral types to become established. Thus it is possible, under certain circumstances, for a fluctuating environment to actually promote an increase in species diversity.

iv. Diversity decrease in a fluctuating environment

The abrupt falls in the diversity trends for Sites 3A, 3B, 3C, 5, 8A, and 8B (H' values, text-figs. 6 and 14) would seem to be due to the effects of localized dominance. Small clearings are continually created on reefs (as outlined above) and in theory these can then be colonized by any available species. However, on most shallow-water reefs such clearings will be rapidly colonized by certain coral types such as the faster-growing ones, or those with more efficient means of dispersal. One or a small number of such types will rapidly pre-empt the greater part of the available habitat space and effectively preclude other corals: as a direct consequence diversity drops sharply. *Acropora* species acted as dominants at Sites 3C, 5, 8A, and 8B, *Galaxea fascicularis* at Site 3B and doming-massive faviids at Site 3A.

No attempt has yet been made to study longer-term diversity trends in the reef. Theoretical arguments predict a steady increase in diversity through succession, followed by a levelling-off when the equilibrium number of species (or climax assemblage) for a particular area is reached (e.g. Odum 1969; Simberloff and Wilson 1969; Grigg and Maragos 1974; Osman and Whitlatch 1978). By increasing the size of quadrats and incorporating data from recent assemblages, it may be possible to document the point at which such asymptotic levelling occurs for various reef environments. Data from sites such as 6 and 28 (text-figs. 6 and 9) suggest that equilibria may perhaps be attained within as little as 2 m of vertical development. At both these sites, the 'equilibrium' number of species in the assemblage would appear to be approximately 20 (text-figs. 6 and 9).

Other factors influencing succession

It was stated in the introduction that the main reef limestones of the Kenya coast are believed to be the product of a single depositional event during the last Interglacial. Although conditions are thought to have been relatively constant during this event, it is likely that minor fluctuations in water depth (and thus in parameters such as the intensity of water movement) constantly occurred. Consequently, it could be argued that some of the trends described in this study reflect no more than a gradual change in coral faunas in response to an environmental gradient (such as increasing water depth). This is particularly so at sites where early constructional domes are replaced by a later mixed-coral framework. Might not these early domes indicate reef development in a comparatively shallow, high-energy environment, and the later framework development in a progressively deeper, quieter-water environment? This could indeed be the case, but it is here maintained that

extrinsic factors can at best only be partially responsible for any of the observed faunal trends. All environments tend to fluctuate, and all but the swiftest successions must take place in a relatively inconstant environment. In practice it has proved extremely difficult to separate the roles of intrinsic and extrinsic factors in ecological successions and thus to assess their relative importance (Kershaw 1973, p. 42; Odum 1971, p. 255; Walker and Alberstadt 1975, p. 238). Taking into account both sedimentary and faunal evidence, it seems unlikely that extrinsic factors exerted any undue influence on any of the trends described here.

Obviously other organisms must play an important part in determining the course of reef succession, but their effects are usually hard to assess in the fossil record. Other sessile organisms (soft corals, algae, sponges, etc.) will compete with corals for the occupancy of available habitat space and patterns of coral distribution and colonization could be seriously disrupted by the activity of predators.

The demonstration of interspecific aggression between scleractinian corals (Lang 1971, 1973; Connell 1973, 1976) has important implications for successional studies as it has been shown that on certain reefs corals can be arranged into natural aggressive hierarchies or 'pecking orders'. However, little work has yet been carried out on the aggressive hierarchies of Indo-Pacific corals.

CONCLUSIONS

In studies of fossil reef succession, geologists should concentrate less on establishing successive zones or stages and more on examining the roles of individual species. Theories based on community-control, i.e. the notion that one set of species in some way 'prepares the ground' for the next, have now been largely superseded by theories based on the interactions of individuals with each other and with the physical environment.

Community-control (or obligatory) succession can, however, be observed in the earliest stages of reef development on a bare substrate. Pioneer assemblages of tolerant and robust corals form low but distinct mounds that are subsequently colonized by assemblages dominated by more sensitive species. Prominent among the latter are many faster-growing branching and platy-encrusting types.

The lack of clear-cut stages (or zones) in the sections studied reflects the random nature of reef succession. Theories based on extrinsic as opposed to intrinsic community-controls predict that any available species can colonize an opening on an established reef and, in time, random, unstructured faunal sequences may be built up.

However, there is some pattern to the early stages of reef succession, as early colonizers are replaced by later arrivals. Competitive interactions occur between individuals and there is evidence that many pioneer species are replaced by faster-growing branching and platy-encrusting types. The principal short-term successional trend in many shallow-water reefs (i.e. those in approximately the 2–10 m depth range) appears to be fairly rapid domination by *Acropora* assemblages.

Longer-term trends are harder to discern but there is some evidence to suggest that, if left undisturbed, many reefs will eventually be dominated by large doming-massive and encrusting colonies. In time, *Acropora*-dominated assemblages could be replaced by massive faviid and poritid assemblages.

There are no consistent short-term diversity trends in the Kenya Pleistocene reef. Adjacent sites show contrasting trends and there is evidence that patterns of species diversity are strongly controlled by localized environmental conditions. Longer-term trends have yet to be fully investigated, but it is possible that in some areas equilibrium assemblages were established within 2 m of vertical development.

Acknowledgements. This work was carried out during the tenure of a N.E.R.C. research studentship, which I gratefully acknowledge. I would also like to express my sincere thanks to the Chairman and Trustees of the Leverhulme Trust for the generous provision of a Royal Society Leverhulme Studentship.

My research was a joint project between the Department of Geology, King's College, London and the British Museum (Natural History). I would like to thank Dr. J. A. E. B. Hubbard (King's College) for her

help and encouragement at all stages of the work and Drs. P. F. S. Cornelius, B. R. Rosen, and J. D. Taylor for facilities extended at the B.M.(N.H.). I had many useful discussions with Dr. Taylor on coral reef diversity problems and Dr. Rosen kindly assisted with the coral taxonomy. British Petroleum allowed me access to unpublished company reports in both Kenya and England. Mr. R. F. Linton (Mombasa) and Drs. W. J. Clarke and R. Walters (Sunbury) were most helpful.

Finally, I would like to thank the Kenya Government and the Director of the Mines and Geological Department, Nairobi for permission to work in Kenya.

REFERENCES

- ALBERSTADT, L. P. and WALKER, K. R. 1976. A receptaculitid-echinoderm pioneer community in a Middle Ordovician reef. *Lethaia*, **9**, 261-272.
- BARNES, D. J. 1973. Coral Reef Project—Papers in Memory of Dr. Thomas F. Goreau. 12. Growth in colonial scleractinians. *Bull. mar. Sci.* **23**, 280-298.
- BRAITHWAITE, C. J. R. 1971. Seychelles reefs: structure and development. *Symp. zool. Soc. Lond.* **28**, 39-63.
- TAYLOR, J. D. and KENNEDY, W. J. 1973. The evolution of an atoll: the depositional and erosional history of Aldabra. *Phil. Trans. R. Soc. Lond.* **B 266**, 307-340.
- BRETSKY, P. W. and BRETSKY, S. S. 1975. Succession and repetition of Late Ordovician fossil assemblages from the Nicolet River Valley, Quebec. *Paleobiology*, **1**, 225-237.
- 1976. The maintenance of evolutionary equilibrium in Late Ordovician benthic marine invertebrate faunas. *Lethaia*, **9**, 223-233.
- BROOK, G. 1893. *Catalogue of the madreporarian corals in the British Museum (Natural History) 1: The genus Madrepora*. London, British Museum (Natural History).
- CLEMENTS, F. E. 1916. Plant succession: an analysis of the development of vegetation. *Publs Carnegie Instn.* **242**, 1-512.
- 1936. Nature and structure of the climax. *J. Ecol.* **24**, 252-284.
- COLINVAUX, P. A. 1973. *Introduction to ecology*. John Wiley & Sons Inc., New York, 621 pp.
- CONNELL, J. H. 1973. Population ecology of reef-building corals. In JONES, E. O. and ENDEAN, R. (eds.). *Biology and geology of coral reefs Volume 2 Biology 1*. Academic Press, New York, 205-245.
- 1976. Competitive interactions and the species diversity of corals. In MACKIE, G. O. (ed.). *Coelenterate ecology and behaviour*. Plenum, New York and London, 51-58.
- 1978. Diversity in tropical rain forests and coral reefs. *Science, N.Y.* **199**, 1302-1310.
- and SLATYER, R. O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* **111**, 1119-1144.
- CRAME, J. A. 1977. Succession and diversity in the Pleistocene coral reefs of the Kenya coast. Unpublished Ph.D. thesis, University of London.
- CROSSLAND, C. 1902. The coral reefs of Zanzibar. *Proc. Camb. phil. Soc. math. phys. Sci.* **11**, 493-503.
- 1903. The coral reefs of Pemba Island and of the East African mainland. *Ibid.* **12**, 36-43.
- 1928. Notes on the ecology of the reef-builders of Tahiti. *Proc. zool. Soc. Lond.* **1928**, 717-735.
- DAVIES, P. S., STODDART, D. R. and SIGEE, D. C. 1971. Reef forms of Addu Atoll, Maldives Islands. *Symp. zool. Soc. Lond.* **28**, 217-259.
- DRURY, W. H. and NISBET, I. C. T. 1973. Succession. *J. Arnold Arbor.* **54**, 331-368.
- EGLER, F. E. 1954. Vegetation science concepts. 1. Initial floristic composition; a factor in old-field vegetation development. *Vegetatio*, **4**, 412-417.
- FROST, S. H. and LANGENHEIM, R. L. 1974. *Cenozoic reef biofacies. Tertiary larger Foraminifera and scleractinian corals from Chiapas, Mexico*. Northern Illinois University Press, De Kalb, Illinois, 387 pp.
- GLEASON, H. A. 1926. The individualistic concept of the plant association. *Bull. Torrey bot. Club.* **53**, 7-26.
- GLYNN, P. W., STEWART, R. H. and MCCOSKER, J. E. 1972. Pacific coral reefs of Panamá: structure, distribution and predators. *Geol. Rdsch.* **61**, 483-519.
- GOLLEY, F. B. 1977. Editor's comments on papers 17 to 21. In GOLLEY, F. B. (ed.). *Ecological succession. Benchmark papers in ecology—5*. Dowden Hutchinson & Ross Inc., Stroudsburg, Pennsylvania, 326-329.
- GOODMAN, D. 1975. The theory of diversity-stability relationships in ecology. *Q. Rev. Biol.* **50**, 237-266.
- GOREAU, T. F. 1959. The ecology of Jamaican coral reefs. I. Species composition and zonation. *Ecology*, **40**, 67-90.

- GOREAU, T. F. 1961. Problems of growth and calcium deposition in reef corals. *Endeavour*, **20**, 32–39.
- 1963. Calcium carbonate deposition by coralline algae and corals in relation to their roles as reef builders. *Ann. N.Y. Acad. Sci.* **109**, 127–167.
- and YONGE, C. M. 1968. Coral community on muddy sand. *Nature, Lond.* **217**, 421–423.
- GOULD, S. J. 1976. Palaeontology plus ecology as palaeobiology. In MAY, R. M. (ed.). *Theoretical ecology: principles and applications*. Blackwell, Oxford, 218–236.
- GOULDEN, C. E. 1969. Temporal changes in diversity. In WOODWELL, G. M. and SMITH, H. H. (eds.). *Diversity and stability in ecological systems*. Brookhaven Symp. Biol. **22**, 96–102.
- GRASSLE, J. F. 1973. Variety in coral reef communities. In JONES, E. O. and ENDEAN, R. (eds.). *Biology and geology of coral reefs Volume 2 Biology 1*. Academic Press, New York, 247–270.
- GRAVIER, C. 1910. Sur la lutte pour l'existence chez les madreporaires des récifs coralliens. *C. r. hebdom. Séanc. Acad. Sci., Paris*, **151**, 955–956.
- GRIFF, R. W. and MARAGOS, J. E. 1974. Recolonization of hermatypic corals on submerged lava flows in Hawaii. *Ecology*, **55**, 387–395.
- GRIME, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* **111**, 1169–1194.
- HORN, H. S. 1974. The ecology of secondary succession. *A. Rev. Ecol. Syst.* **5**, 25–37.
- 1975. Markovian properties of forest succession. In CODY, M. L. and DIAMOND, J. M. (eds.). *Ecology and evolution of communities*. Belknap Press, Cambridge, Mass., 196–211.
- 1976. Succession. In MAY, R. M. (ed.). *Theoretical ecology: principles and applications*. Blackwell, Oxford, 187–204.
- HURLBERT, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, **52**, 577–586.
- JOHNSON, R. G. 1972. Conceptual models of benthic marine communities. In SCHOPF, T. J. M. (ed.). *Models in paleobiology*. Freeman-Cooper, San Francisco, California, 148–159.
- KERSHAW, K. A. 1973. *Quantitative and dynamic plant ecology* (Second Edition). Edward Arnold, London, 308 pp.
- LANG, J. C. 1971. Interspecific aggression by scleractinian corals. 1. The rediscovery of *Scolymia cubensis* (Milne-Edwards and Haime). *Bull. mar. Sci.* **21**, 952–959.
- 1973. Coral Reef Project—Papers in Memory of Dr. Thomas F. Goreau. 11. Interspecific aggression by scleractinian corals. 2. Why the race is not only to the swift. *Ibid.* **23**, 260–279.
- LLOYD, M. and GHELARDI, R. J. 1964. A table for calculating the 'equitability' component of species diversity. *J. Anim. Ecol.* **33**, 217–225.
- LOUCKS, O. L. 1970. Evolution of diversity, efficiency and community stability. *Am. Zool.* **10**, 17–25.
- LOWENSTAM, H. A. 1950. Niagaran reefs of the Great Lakes area. *J. Geol.* **58**, 430–487.
- 1957. Niagaran reefs in the Great Lakes area. In LADD, H. S. (ed.). *Treatise on marine ecology and paleoecology*, 2, *paleoecology*. Mem. geol. Soc. Am. **67**, 215–248.
- LOYA, Y. 1972. Community structure and species diversity of hermatypic corals at Eilat, Red Sea, *Mar. Biol. Berlin*, **13**, 100–123.
- 1976a. The Red Sea coral *Stylophora pistillata* is an r strategist. *Nature, Lond.* **259**, 478–480.
- 1976b. Settlement, mortality and recruitment of a Red Sea scleractinian coral population. In MACKIE, G. O. (ed.). *Coelenterate ecology and behaviour*. Plenum Press, New York and London, 89–99.
- 1976c. Recolonization of Red Sea corals affected by natural catastrophes and man-made perturbations. *Ecology*, **57**, 278–289.
- MACARTHUR, R. H. and CONNELL, J. H. 1966. *The biology of populations*. John Wiley & Sons, Inc., London, 200 pp.
- and WILSON, E. O. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, N.J., 203 pp.
- MANTON, S. M. 1935. Ecological surveys of coral reefs. *Scient. Rep. Gt. Barrier Reef Exped.* **3**, 273–312.
- MARAGOS, J. E. 1974a. Reef corals of Fanning Island. *Pacif. Sci.* **28**, 247–255.
- 1974b. Coral communities on a seaward reef slope, Fanning Island. *Ibid.* **28**, 257–278.
- MARGALEF, D. R. 1968. *Perspectives in ecological theory*. University of Chicago Press, Chicago, 111 pp.
- MARSHALL, S. M. and ORR, A. P. 1931. Sedimentation on Low Isles and its relation to coral growth. *Scient. Rep. Gt. Barrier Reef Exped.* **1**, 93–133.
- MATTHAI, G. 1914. A revision of the Recent colonial Astracidae possessing distinct corallites. (Based on material from the Indo-Pacific Ocean and the collections of Paris, Berlin, Vienna, Copenhagen, London and Glasgow). *Trans. Linn. Soc. Lond. (Zool.)*, **17**, 1–140.

- MAXWELL, W. G. H. 1968. *Atlas of the Great Barrier Reef*. Elsevier, Amsterdam. 285 pp.
- MAY, R. M. 1973. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, N.J., 265 pp.
- 1975. Patterns of species abundance and diversity. In CODY, M. L. and DIAMOND, J. M. (eds.). *Ecology and evolution of communities*. Belknap Press, Cambridge, Mass., 81–120.
- MAYOR, A. G. 1918. Ecology of the Murray Island coral reef. *Pap. Dep. mar. Biol. Carnegie Instn Wash.* **9**, 1–48.
- 1924. Structure and ecology of Samoan reefs. *Ibid.* **19**, 1–25.
- MERGNER, H. and SCHEER, G. 1974. The physiographic zonation and the ecological conditions of some south Indian and Ceylon coral reefs. In CAMERON, A. M. *et al.* (eds.). *Proceedings of the Second International Coral Reef Symposium*. 2. Great Barrier Reef Committee, Brisbane, Queensland, 2–30.
- MESOLELLA, K. J., SEALY, H. A. and MATTHEWS, R. K. 1970. Facies geometries within Pleistocene reefs of Barbados, West Indies. *Bull. Am. Ass. Petrol. Geol.* **54**, 1899–1917.
- NICOL, D. 1962. The biotic development of some Niagaran reefs—an example of an ecological succession or sere. *J. Paleont.* **36**, 172–176.
- ODUM, E. P. 1969. The strategy of ecosystem development. *Science, N.Y.*, **164**, 262–270.
- 1971. *Fundamentals of ecology* (Third Edition). W. B. Saunders, Philadelphia, 574 pp.
- OLSON, J. S. 1958. Rates of succession and soil changes on southern Lake Michigan dunes. *Bot. Gaz.* **119**, 125–170.
- OSMAN, R. W. and WHITLACH, R. B. 1978. Patterns of species diversity: fact or artifact? *Paleobiology*, **4**, 41–54.
- PICHON, M. 1974. Free living scleractinian coral communities in the coral reefs of Madagascar. In CAMERON, A. M. *et al.* (eds.). *Proceedings of the Second International Coral Reef Symposium*. 2. Great Barrier Reef Committee, Brisbane, Queensland, 173–181.
- PIELOU, E. C. 1975. *Ecological diversity*. John Wiley & Sons, London, 165 pp.
- PORTER, J. W. 1972a. Predation by *Acanthaster* and its effect on coral species diversity. *Am. Nat.* **106**, 487–492.
- 1972b. Patterns of species diversity in Caribbean reef corals. *Ecology*, **53**, 745–748.
- ROSEN, B. R. 1968. An account of a pathological structure in the Faviidae (Anthozoa): a revision of *Favia valenciennesi* (Edwards and Haime) and its allies. *Bull. Br. Mus. nat. Hist. (Zool.)*, **16**, 323–352.
- 1971. Principal features of reef coral ecology in shallow water environments of Mahé, Seychelles. *Symp. zool. Soc. Lond.* **28**, 163–183.
- 1972. Recent reef corals of the Seychelles with particular reference to the island of Mahé. Unpublished Ph.D. thesis, University of London.
- 1975. The distribution of reef corals. *Rep. Underwater Ass.* **1**, 1–16.
- SIMBERLOFF, D. S. and WILSON, E. O. 1969. Experimental zoogeography of islands. The colonisation of empty islands. *Ecology*, **50**, 278–314.
- STIMSON, J. 1974. An analysis of the pattern of dispersion of the hermatypic coral *Pocillopora meandrina* var. *nobilis* Verrill. *Ibid.* **55**, 445–449.
- STODDART, D. R. 1969. Ecology and morphology of recent coral reefs. *Biol. Rev.* **44**, 433–498.
- 1973. Coral reefs in the Indian Ocean. In JONES, O. A. and ENDEAN, R. (eds.). *Biology and geology of coral reefs Volume 1 Geology 1*. Academic Press, New York, 51–92.
- TALBOT, F. H. 1965. A description of the coral structure of Tutia Reef (Tanganyika Territory, East Africa) and its fish fauna. *Proc. zool. Soc. Lond.* **145**, 431–470.
- TANSLEY, A. G. 1935. The use and abuse of vegetational terms and concepts. *Ecology*, **16**, 284–307.
- UMBROGROVE, J. H. F. 1947. Coral reefs of the East Indies. *Bull. geol. Soc. Am.* **58**, 729–778.
- VALENTINE, J. W. 1973. *Evolutionary paleoecology of the marine biosphere*. Prentice-Hall Inc., Englewood Cliffs, N.J., 511 pp.
- VAUGHAN, T. W. 1918. Some shoal-water corals from Murray Island (Australia), Cocos-Keeling Islands and Fanning Island. *Pap. Dep. mar. Biol. Carnegie Instn Wash.* **9**, 51–234.
- and WELLS, J. W. 1943. Revision of the suborders, families and genera of the Scleractinia. *Spec. Pap. geol. Soc. Am.* **44**, 363 pp.
- WALKER, K. R. and ALBERSTADT, L. P. 1975. Ecological succession as an aspect of structure in fossil communities. *Paleobiology*, **1**, 238–257.
- and PARKER, W. C. 1976. Population structure of a pioneer and a later stage species in an Ordovician ecological succession. *Ibid.* **2**, 191–201.
- WELLS, J. W. 1954. Recent corals of the Marshall Islands. *Prof. Pap. U.S. geol. Surv.* **260 I**, 385–486.
- WHITTAKER, R. H. 1975. *Communities and ecosystems* (Second Edition). Macmillan, New York, 385 pp.

- WIJSMAN-BEST, M. 1972. The systematics and ecology of New Caledonia Faviinae. *Bijdr. Dierk.* **42**, 1-76.
- 1974. Habitat-induced modification of reef corals (Faviidae) and its consequence for taxonomy. In CAMERON, A. M. *et al.* (eds.). *Proceedings of the Second International Coral Reef Symposium*. 2. Great Barrier Reef Committee, Brisbane, Queensland, 217-228.
- YONGE, C. M. 1973. Coral Reef Project—Papers in Memory of Dr. Thomas F. Goreau. 1. The nature of reef-building (hermatypic) corals. *Bull. mar. Sci.* **23**, 1-15.

J. A. CRAME

British Antarctic Survey
Natural Environment Research Council
Madingley Road
Cambridge CB3 0ET

Typescript received 15 January 1979

Revised typescript received 2 April 1979

APPENDIX

NOTES ON CORAL NOMENCLATURE AND SPECIES GROUPING

- Pocillopora* sp. gp. 1: the more delicate branching forms of *Pocillopora*; generally small colonies; this group embraces both delicate forms such as *P. damicornis* (Linnaeus) and more robust species such as *P. danae* Verrill and *P. meandrina* Dana (cf. Rosen 1971, p. 169).
- Pocillopora* sp. gp. 2: forms with stouter, longer branches; generally larger colonies; typified by *P. eydouxi* Milne-Edwards and Haime.
- Acropora* sp. gp. 1: the *A. humilis* (Dana) group, following the interpretation of *A. humilis* by Wells (1954, p. 425).
- Acropora* sp. gp. 2: the *A. hyacinthus* (Dana) group, based on the descriptions of the species *M. (Madrepora, later Acropora) cytherea* Dana, *M. armata* Brook, *M. hyacinthus*, and *M. reticulata* Brook by Brook (1893); see also the grouping of *A. hyacinthus*, *A. cytherea*, and *A. reticulata* by Wells (1954, p. 422). Somewhat less satisfactorily, forms resembling *A. irregularis* (Brook) have also been included in this group. A short working definition of the group is as follows: small colonies with short, thin, pointed branches; each branch giving rise to several side branches; colony shape either corymbose or horizontally branching.
- Very large colonies of *A. hyacinthus* also occur; in particular, large, thick-sheet form colonies occur in shallow, protected sites on a number of reefs (e.g. Talbot 1965; Braithwaite *et al.* 1973).
- Acropora* sp. gp. 3: *Acropora* of the types covered by groups 1 and 2 but not well enough preserved to be confidently assigned to either of these groups.
- Acropora* sp. gp. 4: stagshorn *Acropora*; principally *A. formosa* (Dana) (Wells 1954, p. 415; see also Rosen 1971, p. 172).
- Acropora* sp. gp. 6: the *A. conferta* group (see Brook 1893, p. 108); colony bases formed of a mesh of horizontal branches; short, spiky upright branches rise up from the base.
- Acropora* sp. gp. 7: platy-encrusting *Acropora* that cannot be readily grouped with other platy-encrusting types (i.e. the platy-encrusting forms of *A. hyacinthus* or *A. palifera*); plate thickness generally less than 3 cm.
- Acropora* sp. gp. 8: thick-encrusting and massive *Acropora* that cannot be definitely assigned to the *A. palifera* (Lamarck) group.
- A. palifera*: included in this group is *A. cuneata* (Dana), a form which closely resembles *A. palifera* (Wells 1954, pp. 429-431). Brook's descriptions of the species comprising his subgenus *Isopora* (*M. palifera*, *M. palifera* var. α , *M. hispida* Brook, *M. securis* Dana, *M. cuneata* Dana, and *M. plicata* Brook) were also used in the determination of this group (Brook 1893, p. 131).
- A. palifera* gp. 1: embracing both *A. palifera* forma α and *A. palifera* forma β of Wells (1954); the thick-branching types.
- A. palifera* gp. 2: a rather unusual group that has distinctly platy colonies; generally no more than 3 cm thick; some plates are up to 1 m across; the exact systematic status of this group is uncertain.
- A. palifera* gp. 3: thick, massive-encrusting types.
- A. palifera* gp. 4: a form with prominent 'blades' rising from a hummocky base; closely resembling the holotype of *A. securis* (Dana) (Wells 1954, pl. 133) (which is now included in *A. cuneata* (Dana)—Wells 1954, p. 429).

- Porites* sp. gp. 1: the branching species of *Porites*; principally forms that closely resemble both *P. andrewsi* Vaughan and *P. nigrescens* Dana.
- Porites* sp. gp. 2: the massive species of *Porites*; principally forms that resemble species such as *P. lutea* Milne-Edwards and Haime and *P. solida* (Forskål).
- Favia*: accurate identification of the various species within this genus proved to be extremely difficult. Even though numerous descriptions of the principal large-calice forms are available (e.g. Matthai 1914; Vaughan 1918; Wells 1954; Rosen 1968; Wijsman-Best 1972), it was impossible to divide the specimens from the Kenya Pleistocene reef into meaningful species groups. The three commonest large-calice species, *F. favius* (Forskål), *F. speciosa* (Dana), and *F. pallida* (Dana), are here combined as *Favia* sp. gp. 1. *F. stelligera* (Dana), by virtue of both its growth form and calical configuration, is a distinctive species (see, e.g., Vaughan 1918, p. 101).
- Leptastrea* sp. gp. 2: principally *L. bottae* (Milne-Edwards and Haime) and *L. immersa* Klunzinger; a group with large, prominent, subcircular calices.